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Island Biogeography in the Anthropocene and Quaternary

" Documento Definitivo"

Doutoramento em Biodiversidade, Genética e Evolução

Sietze Johannes Norder

Tese orientada por:

Doutora Margarida Maria Demony de Carneiro Pacheco de Matos
Doutor Paulo Alexandre Vieira Borges
Doutor Kenneth Frank Rijsdijk

Documento especialmente elaborado para a obtenção do grau de doutor

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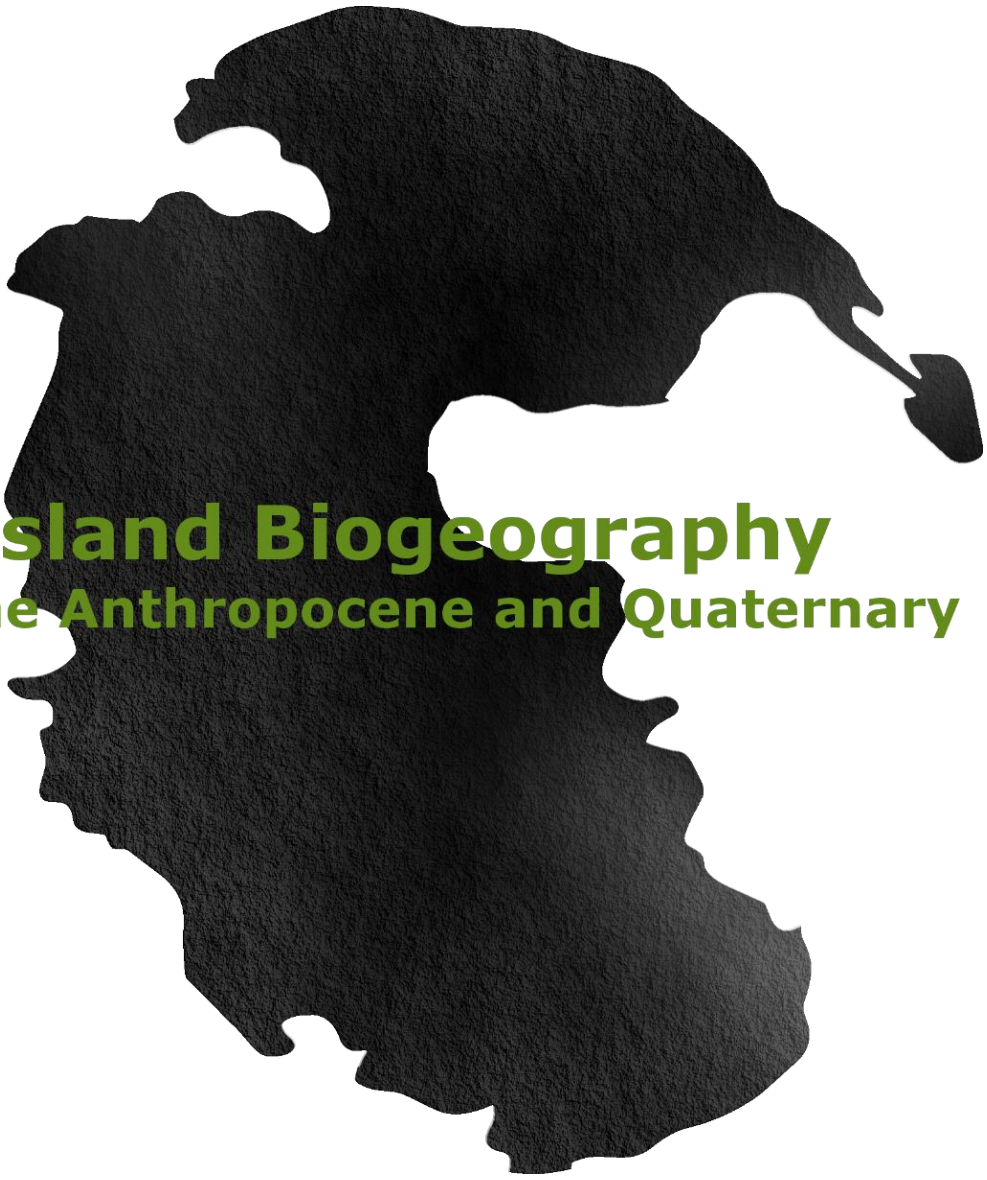

Island Biogeography

in the Anthropocene and Quaternary

NOTA PRÉVIA

A presente tese apresenta resultados de trabalhos já publicados ou em preparação para publicação (Parte 1 e 2), de acordo com o previsto no nº 2 do artigo 25º do regulamento de Estudos Pós-graduados da Universidade de Lisboa, publicado no Diário de República II série nº 57 de 23 de Março de 2015. Tendo os trabalhos sido realizados em colaboração, o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, Fevereiro de 2020

Sietze Johannes Norder

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ABSTRACT

The realization that human activities have a major influence on ecosystems from local to global scales has given rise to the concept of the Anthropocene. However, although the influence of human activities on biodiversity is clearly significant, it remains unclear to what extent the rate and magnitude of biodiversity changes differ from pre-human dynamics. Islands are ideal model systems for understanding the relative contribution of environmental and societal variables to biodiversity change because the onset of human activities on islands can generally be clearly defined. The aim of this PhD thesis is to place human-environment interactions on islands in the context of environmental fluctuations over the Quaternary. The thesis consists of two parts. First, I quantify how island area and isolation have changed over the Quaternary as a result of climate-driven sea-level fluctuations, and analyse how these dynamics have shaped modern biodiversity patterns. Secondly, I study how human activities in the past and present have shaped island ecosystems and landscapes, and compare their rate and magnitude to pre-human dynamics. Overall, the findings of my thesis indicate that modern biodiversity patterns show legacies of past human activities but are also imprinted by environmental dynamics in deep-time. Furthermore, the rate of change following human settlement on islands can largely exceed Quaternary background rates. Therefore, my findings are in line with studies that indicate that human activities have become a major driver in shaping biodiversity across scales. Nonetheless, my comparison of islands worldwide also highlights the diverse ways in which abiotic, biotic, and anthropogenic variables have interacted across individual islands. Therefore, future studies should acknowledge that global biodiversity change can manifest differently across localities. Finally, I emphasize the importance of strengthening interdisciplinary approaches in island biogeography to enhance our understanding of biodiversity changes in the Anthropocene, and how they relate to deep-time dynamics.

Key words

Volcanic oceanic islands, social-ecological systems, glacial-interglacial cycles, human ecodynamics, biodiversity

RESUMO

A constatação de que as atividades humanas exercem uma grande influência sobre os ecossistemas, da escala local à global, originou o conceito do Antropoceno. No entanto, apesar da influência das atividades humanas ser claramente significativa, ainda não está claro até que ponto a taxa e magnitude de alterações na biodiversidade diferem da dinâmica pré-humana. As ilhas constituem sistemas modelo ideais para compreender a contribuição relativa de variáveis ambientais e sociais, porque o início das atividades humanas é em geral conhecido. O objetivo desta tese de doutoramento é enquadrar as interações homem-ambiente nas ilhas no contexto das flutuações ambientais no Quaternário. A tese consiste em duas partes. Primeiro, quantifico como a área da ilha e o isolamento mudaram no Quaternário devido às flutuações do nível do mar provocadas pelo clima e analiso como essas dinâmicas moldaram os padrões modernos de biodiversidade. Em segundo lugar, estudo como as atividades humanas passadas e presentes moldaram os ecossistemas e paisagens das ilhas e comparo a sua taxa e magnitude com a dinâmica pré-humana. As conclusões de minha tese indicam que os padrões modernos de biodiversidade mostram legados de atividades humanas passadas, mas também são afectados pela dinâmica ambiental em escalas temporais longinquas. Além disso, a taxa de alterações após o povoamento humano nas ilhas pode exceder largamente taxas quaternárias antecedentes. Os meus resultados concordam com estudos mostrando que as atividades humanas têm sido um fator importante na modelação da biodiversidade ao longo do tempo. Mas a minha comparação global de ilhas também destaca diversas maneiras pelas quais variáveis abióticas, bióticas e antropogénicas interagiram entre ilhas. Estudos futuros devem reconhecer que a mudança global da biodiversidade pode manifestarse de formas diferente entre localidades. Por fim, destaco a importância de aumentar abordagens interdisciplinares na biogeografia insular para melhor compreender as mudanças da biodiversidade no Antropoceno.

Palavras-chave:

Ilhas oceânicas vulcânicas; sistemas socio-ecológicos; ciclos glaciares-interglaciares, Ecodinâmica humana, biodiversidade

RESUMO ALARGADO

Os padrões de biodiversidade e o funcionamento dos ecossistemas são cada vez mais moldados pelas atividades humanas em diferentes escalas, da escala local à global. O que permanece pouco claro, contudo, é como é que a taxa e a magnitude das mudanças induzidas pelo homem se relacionam com a dinâmica pré-humana. Antes do Homo sapiens emergir em África, o mundo já não era um lugar estático: os climas alternavam entre períodos quentes e frios, e massas terrestres inteiras emergiam e desapareciam. Essa dinâmica ambiental de longo prazo preparou o terreno para a evolução de espécies, ecossistemas e sociedades humanas. O objetivo geral da minha tese de doutoramento é, portanto, de comparar a contribuição relativa da dinâmica humana e ambiental no passado e no presente para moldar os padrões modernos de biodiversidade. Em grandes escalas espaciais essa comparação pode constituir um grande desafio, porque os fatores ambientais e sociais interagem de forma complexa, e.g. dada a incerta/variável intervenção inicial humana. Em ilhas oceânicas, no entanto, o início das atividades humanas é em geral definido de forma relativamente precisa, tornando-as sistemas-modelo ideais para estudar as consequências da biodiversidade da dinâmica humana e ambiental ao longo do tempo. A minha investigação foca a biogeografia das ilhas, uma disciplina que procura entender como variam os padrões de biodiversidade entre e dentro das ilhas, assim como as causas dessa variação. No entanto, antes de aprofundar temáticas que investigo na minha tese, inicio com uma **Introdução Geral** sobre como os padrões de biodiversidade em todo o mundo foram moldados ao longo do tempo por fatores antropogénicos e ambientais. Posteriormente, defino as questões que guiam a minha tese, perguntando como os fatores antropogénicos e ambientais envolvidos na mudança da biodiversidade se manifestam nas ilhas e como eles interagem. Para abordar essas questões, estruturei a tese em duas partes, cada uma explorando a dinâmica biogeográfica nas ilhas, mas em escalas de tempo muito diferentes. Na primeira parte, 'Biogeografia das ilhas no Quaternário' (**'Island Biogeography in the Quaternary'**), concentro-me na dinâmica biogeográfica nos últimos 2,58 milhões de anos para compreender as mudanças a longo prazo na geografia das ilhas e de que forma afetaram os padrões modernos de biodiversidade. Na segunda parte, 'Biogeografia de ilhas no Antropoceno' (**'Island Biogeography in the Anthropocene'**), estudo a importância relativa de fatores antropogénicos e ambientais na modelação de ecossistemas e paisagens de ilhas nos últimos milénios a séculos.

A **Parte 1** é constituída por duas secções que juntas analisam até que ponto os padrões modernos de biodiversidade nas ilhas foram moldados por mudanças geográficas do passado.

Ao longo de escalas de tempo que vão de milhões de anos a milénios, as ilhas oceânicas são entidades altamente dinâmicas. Elas emergem e submergem, encolhem e expandem, dividem-se e afundam-se devido às flutuações do nível do mar provocadas pelo clima. No entanto, até recentemente, não se sabia até que ponto essas flutuações do nível do mar no Quaternário afetaram as características geográficas das ilhas, tais como a área e grau de isolamento das ilhas. Tendo isso em conta, na **secção 1.1** quantifico as mudanças provocadas pelo nível do mar na geografia das ilhas e na configuração de arquipélagos para 178 ilhas distribuídas em 27 arquipélagos em todo o mundo. Deste estudo resultou a base de dados 'Palaeo-Islands and Archipelago Configuration' (PIAC), o primeiro de seu tipo. Os dados mostram que cada ilha tem uma resposta única às flutuações do nível do mar, principalmente devido a diferenças na batimetria (topografia subaquática). A quantificação dessas dinâmicas para ilhas individuais permitiu investigar o papel da geografia do passado na formação dos padrões modernos de biodiversidade. Na **secção 1.2** usamos essa base de dados para explorar até que ponto os padrões modernos de biodiversidade evidenciam marcas das configurações dos arquipélagos no passado. Estudos anteriores que exploraram essa relação geralmente focaram-se num período limitado no tempo: o baixo nível do mar, de curta duração, no Último Máximo Glacial. Como essas condições são altamente excecionais em comparação com as flutuações do nível do mar nos últimos milhões de anos, considerámos muito pertinente explorar o papel das configurações dos arquipélagos mais representativas no Quaternário. Com este objetivo, avaliámos o efeito de seis configurações alternativas de arquipélagos na distribuição moderna de moluscos terrestres e angiospérmicas, envolvendo 53 ilhas distribuídas em oito arquipélagos em todo o mundo. Constatamos que os padrões de riqueza específica nestes dois taxa de espécies endémicas exclusivas de uma única ilha são moldados principalmente por configurações dos arquipélagos correspondentes a níveis do mar representativos do Quaternário. Por outro lado, o efeito de condições excecionais e de curta duração, como o Último Máximo Glacial, nos padrões modernos de biodiversidade foi geralmente fraco. As nossas observações revelam a importância do legado de dinâmicas geográficas do passado l nos padrões modernos de biodiversidade insular.

A **Parte 2** consiste em duas secções que exploram como é que as interações homem-ambiente moldaram os ecossistemas e paisagens das ilhas, e de que modo essas mudanças se relacionam com a dinâmica pré-humana. Na **secção 2.1** apresento um caso de estudo da ilha Maurícia e analiso a evolução das interações homem-ambiente desde o primeiro povoamento humano.

Recorremos à história bem documentada da ilha para modelar a quantidade de perda de solo resultante da desflorestação e comparar as taxas induzidas pelo homem com as taxas geológicas de base. A nossa análise revela que a taxa e magnitude da perda de solo após a chegada humana excede amplamente as condições naturais de base. Solos saudáveis são a base dos ecossistemas e dos serviços que eles fornecem à sociedade. Consequentemente, as elevadas taxas de perda de solo na ilha Maurícia podem comprometer a sustentabilidade a longo prazo do sistema socioecológico. No entanto, encontramos grandes variações na quantidade de perda de solo entre locais da ilha, relacionadas com quando e onde as áreas foram desflorestadas, assim como com as condições ambientais (por exemplo, topografia) que tornam alguns locais mais vulneráveis do que outros à perda de solo. Assim, após este caso de estudo numa única ilha, fizemos um estudo comparativo das interações homem-ambiente em trinta ilhas do Oceano Atlântico (**secção 2.2**). Especificamente, avaliamos como as condições sociais e ambientais contrastantes afetam a extensão da cobertura vegetal nativa nas ilhas. Adotamos uma abordagem interdisciplinar para combinar uma análise estatística dos fatores ambientais e sociais com uma reconstrução qualitativa das tendências históricas da sociedade. Os nossos resultados mostram que as diferenças na cobertura da vegetação nativa entre as ilhas são explicadas em grande parte pela topografia, em particular o grau acidentado dos terrenos, sugerindo que as decisões sociais sobre o uso/mudança na cobertura dos solos são parcialmente motivadas pelas características da paisagem. Estas conclusões ilustram a importância de considerar o contexto da paisagem ao estudar impactos humanos na biodiversidade das ilhas.

Finalmente, ao considerar a tese como um todo, duas conclusões principais emergem. **A primeira conclusão** é que os padrões modernos de biodiversidade mostram legados de atividades humanas passadas, mas também são afetados pela dinâmica ambiental em escalas temporais longínquas. Além disso, as atividades humanas podem moldar a biodiversidade das ilhas de tal maneira que a taxa e magnitude das mudanças envolvidas excede a amplitude de variação no Quaternário. Por exemplo, as taxas de perda de habitat nativo ao longo de alguns séculos de povoamento humano podem exceder até as taxas mais rápidas de perda de área devido ao aumento do nível do mar no Quaternário. No entanto, as atividades humanas não substituem simplesmente os fatores ambientais, mas interagem com eles, e também são afetadas por eles. Isso é ilustrado pela nossa constatação de que os padrões de uso/cobertura do solo nas ilhas são parcialmente modelados pela topografia das ilhas. **Uma segunda conclusão** é que, embora as flutuações do nível do mar no Quaternário e as atividades

humanas tenham moldado os padrões de biodiversidade nas ilhas, também existe uma grande variabilidade entre elas. Assim, embora a biodiversidade se esteja rapidamente a deteriorar globalmente, as mudanças na biodiversidade manifestam-se de maneira diferente entre localidades. Uma melhor compreensão das mudanças sociais e ambientais que promovem impactos heterogéneos sobre a biodiversidade é crucial para o desenvolvimento de estratégias baseadas localmente para a conservação da biodiversidade no Antropoceno.

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Norder S.J., Proios, K.V., Whittaker, R.J., Alonso, M.R., Borges, P.A.V., Borregaard, M.K., Cowie, R.H., Florens, F.B.V., de Frias Martins, A.M., Ibáñez, M., Kissling, W.D., de Nascimento, L., Otto, R., Parent, C.E., Rigal, F., Warren, B.H., Fernández-Palacios, J.M., van Loon, E.E., Triantis, K.A., Rijsdijk, K.F. (2019). Beyond the Last Glacial Maximum: island endemism is best explained by long-lasting archipelago configurations. Global Ecology and Biogeography. https://doi.org/10.1111/geb.12835

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Norder, S.J., de Lima, R.F., de Nascimento, L., Lim, J.Y., Fernández-Palacios, J.M., Romeiras, M.M., Elias, R.B., Cabezas, F.J., Catarino, L., Ceríaco, L.M.P., Castilla-Beltrán, A., Gabriel, R., Menezes de Sequeira, M., Rijsdijk, K.F., Nogué, S., Kissling, W.D., van Loon, E.E., Hall, M., Matos, M., Borges, P.A.V. (in revision). Global change in microcosms: environmental and societal predictors of land cover change on the Atlantic Ocean Islands. Submitted to Anthropocene.

225 Million years ago, all continents were merged into one single island, better known as the supercontinent Pangea. This geographical configuration existed millions of years before the Quaternary and the Anthropocene started. Nonetheless, I present this figure (modified after Norder & Rijsdijk, 2016) because it illustrates the approach I adopt in this thesis: I view islands as microcosms of global change, and explore how past dynamics have shaped our modern world. Full reference: Norder, S.J. & Rijsdijk, K.F. (2016) Interdisciplinary island studies: connecting the social sciences, natural sciences and humanities. Island Studies Journal, 11, 673–686.

GENERAL INTRODUCTION

GLOBAL BIODIVERSITY CHANGES IN THE ANTHROPOCENE

As a consequence of human activities, biodiversity patterns and processes have changed dramatically from local to global scales. Currently, around 75% of Earth's terrestrial surface is altered by human land use (Ellis & Ramankutty, 2008; Venter *et al.*, 2016). As a result of land use change, native habitats have become fragmented and reduced in size (Watson *et al.*, 2016). Globally, land use change is one of the major drivers of biodiversity loss (Newbold *et al.*, 2015, 2016). However, land use change is just one of the drivers of extinction, and interacts with others such as climate change, overexploitation, and invasive species (Maxwell *et al.*, 2016). Current rates of extinction largely exceed geological background rates, bringing a 6th global mass extinction close unless ongoing threats to species are lessened (Barnosky *et al.*, 2011). In addition, population sizes of remaining species show an overall decline of 60% since 1970 (WWF, 2018). Simultaneously, while species richness is rapidly declining at the global scale, at local to regional scales species richness is often increasing due to the introduction of non-native species (Sax & Gaines, 2003; Vellend *et al.*, 2017). Biodiversity patterns are sometimes better explained by socioeconomic drivers than by biophysical factors (Helmus *et al.*, 2014). Today, human activities have become a major driver of changes in the biosphere (Steffen *et al.*, 2015). These impacts will likely leave a trace in the fossil record thousands (Zalasiewicz *et al.*, 2011), and perhaps millions of years from now. The realization that humans have become a major force in shaping the functioning of the Earth system has led to the proposal that we have entered a new geological epoch: the Anthropocene (Crutzen & Stoermer, 2000; Crutzen, 2002). While the Anthropocene has been embraced by scholars from a variety of disciplines as well as by the wider public, it also remains controversial (Malhi, 2017). At the centre of the debate is not whether human activities are affecting the functioning of the Earth system, but rather how and when these changes came into being (Ellis *et al.*, 2016). While global environmental and ecological changes have accelerated over the last decennia to centuries, they are the cumulative outcome of local human-environment interactions in the deeper past (Steffen *et al.*, 2007; Braje & Erlandson, 2013).

HISTORICAL ROOTS OF THE ANTHROPOCENE: LOCAL TRANSFORMATION OF ECOSYSTEMS

With the spread of *Homo sapiens* across the globe, wherever people set foot, they modified their local environment to suit their needs (Boivin *et al.*, 2016). Already ~50.000 years ago,

hunter-gatherer societies drove several large mammals to extinction, including mammoths, giant sloths and rhinoceroses (Araujo *et al.*, 2017). While the disappearance of the Pleistocene megafauna had consequences for the functioning of local ecosystems (Pires *et al.*, 2018), it might have also driven changes in the global climate (Doughty *et al.*, 2010; Malhi *et al.*, 2016). From 12.000-11.000 years ago, hunter-gatherer lifestyles were gradually being replaced by agricultural societies. The domestication of plants and animals started in at least eleven locations across the globe (the Fertile Crescent was one of those; Lawrence *et al.*, 2017), from where it spread to other regions during subsequent millennia (Larson *et al.*, 2014). By three millennia ago, hunter-gatherers and agriculturalists had already modified large parts of Earth's land surface (Stephens *et al.*, 2019). While individual societies already transformed vast tracts of land millennia ago, until the fifteenth century biotic and cultural exchanges were restricted to sub-global scales (Lightfoot *et al.*, 2013). This changed following the arrival of Columbus to the Caribbean and the Americas: the first contact between the Old- and New World breached long-standing geographical barriers creating a "New Pangea" (Mooney & Cleland, 2001; Rosenzweig, 2001). Transoceanic trade over subsequent centuries caused a further reshuffling of Earth's biota and cultures, referred to as the Columbian exchange (Crosby, 1972). Since the origin of our species, people have transformed ecosystems and affected the lives of thousands of other species with whom we share our planet. The actions of our ancestors have left many traces in the biodiversity patterns we observe today (Boivin *et al.*, 2016). Therefore, to understand biodiversity patterns in the Anthropocene we should not only consider modern human impacts, but also explore legacies of human activities in the deeper past.

MODERN BIOGEOGRAPHIC PATTERNS AND QUATERNARY CLIMATE VARIABILITY

Biogeography is the discipline that attempts to understand how and why biodiversity varies across space (Lomolino *et al.*, 2017). Over the last millennia to centuries, human activities have become a global 'geophysical force' (Steffen *et al.*, 2007) in shaping biodiversity patterns. However, anthropogenic drivers are only a recent addition to the suit of environmental drivers that shaped biogeographical processes over much longer timescales. For example, flowering plants, which today account for 96% of the diversity in vascular plants (Schuettpelz & Pryer, 2009), mainly diversified and rose to dominance during the Cretaceous (Crane *et al.*, 1995; Friis *et al.*, 2006). In contrast, the radiation of mammals

mainly took place during the Cenozoic (Leary *et al.*, 2013; Foley *et al.*, 2016), after a meteorite impact wiped out most dinosaurs creating new opportunities for mammals to flourish (Meredith *et al.*, 2011). About 15-12 million years ago, the first hominids, or 'great apes' evolved (Robson & Wood, 2008). These include species of the genus *Pongo* (Orangutans), *Gorilla*, *Pan* (Chimpanzee, Bonobo), and *Homo*. The evolution of the genus *Homo* might have been shaped by climatic fluctuations over the Quaternary (Maslin & Christensen, 2007; Maslin *et al.*, 2014; Potts & Faith, 2015). The Quaternary Period (2.58 million years ago – present) is characterized by glacial-interglacial cycles and coincided with a cooling of the global climate (Head *et al.*, 2008). Quaternary climate changes left a strong imprint on the modern geographical distribution of species (Dynesius & Jansson, 2000; Araújo *et al.*, 2008; Svenning *et al.*, 2015), including our own. Following the emergence of *Homo sapiens* 200.000-400.000 years ago (Hublin *et al.*, 2017), the subsequent spread of people across the world has been related to Quaternary variations in climate and sea level (Carto *et al.*, 2009; Lopes dos Santos *et al.*, 2009; Timmermann & Friedrich, 2016).

ISLANDS: GLOBAL CHANGE IN MICROCOSMS

With the colonization of the Americas around 15.000 years ago (Goebel *et al.*, 2008), all continents except Antarctica became inhabited by people. In contrast, for most oceanic islands it took several thousands of years more before they were settled (Keegan & Diamond, 1987; Cherry & Leppard, 2015). Given the relatively recent colonization of oceanic islands, their entire history of human-environment interactions is compressed into a few millennia to centuries. Nonetheless, despite their relatively short duration of human contact, island ecosystems and landscapes have been radically transformed by human activities (Russell & Kueffer, 2019). Compared to continents, island biodiversity is generally more strongly affected by land use change (Kier *et al.*, 2009; Borges *et al.*, 2019; Sanchez-Ortiz *et al.*, 2019), extinctions (Tershy *et al.*, 2015; Whittaker *et al.*, 2017), and invasive species (Sax & Gaines, 2008; Russell *et al.*, 2017; Spatz *et al.*, 2017). Many of the biodiversity changes on islands have left clear signals in pollen diagrams (Nogué *et al.*, 2017), and have sometimes been documented in historical records (Grove, 1996). Islands have figured prominently as laboratories in the study of human-environment relationships (Kirch, 1997; Kueffer & Kinney, 2017; Dinapoli & Leppard, 2018), but have also greatly contributed to the development of ecological and evolutionary theories (Darwin, 1859; Wallace, 1880; Vitousek, 2002; Warren *et al.*, 2015). Their defined geographical boundaries, relative isolation, and clear onset of human colonization make them ideal model systems for

comparing human impacts on biodiversity to pre-human ecological and environmental conditions. However, before the first human settlers arrived, islands were far from static. Island geography is sculpted over time by volcanism, erosion, and sea-level fluctuations, with implications for biodiversity as well (Whittaker *et al.*, 2008; Fernández-Palacios *et al.*, 2016; Borregaard *et al.*, 2017). Therefore, to better understand the magnitude of human impacts on biodiversity, we should not only compare human activities to a single pre-human baseline, but also consider the range of environmental variability over longer timescales (Willis & Birks, 2006; Nogué *et al.*, 2017). Because climatic fluctuations over the Quaternary have strong legacies on modern biodiversity patterns (Svenning *et al.*, 2015), Quaternary baselines might be particularly suitable to compare human-induced changes with (Froyd & Willis, 2008). Such an approach will help placing human-induced changes in the Anthropocene in their deep-time environmental context.

AIM AND RESEARCH QUESTIONS

The aim of my thesis is twofold: 1) to place human-environment interactions in the context of deep-time biogeographical dynamics, and 2) to understand how environmental and societal conditions, and their interactions, shaped modern biodiversity patterns. Throughout my thesis I will use islands as model systems to explore how biodiversity changes manifest differently across regions and through time. Therefore, the main research question of this thesis is:

How do human-environment interactions on islands relate to

biogeographical dynamics over longer timescales?

I have divided this main question in two sub questions:

1. *To what extent have present-day biodiversity patterns on islands worldwide been shaped by past geographical changes?*
2. *How have human-environment interactions shaped island ecosystems and landscapes?*

STRUCTURE OF THESIS

In part 1 ‘Island Biogeography in the Quaternary’, I focus on the legacies of geographical dynamics of oceanic islands over the Quaternary on modern biodiversity patterns. Before I can start analysing the relationship between geographical dynamics and biodiversity patterns, the geographical dynamics of islands over the Quaternary first need to be quantified. I therefore developed a global spatially-explicit database of changes in island geography and palaeo configuration. The database contains sea-level driven changes in palaeo-geography for

178 oceanic islands in 27 archipelagos spread across the world (section 1.1; Norder *et al.*, 2018). I subsequently use these data to assess to what extent present-day biodiversity patterns can be explained by island geography in the past. Rather than focusing on a single Quaternary baseline, I test for the role of different archipelago configurations in shaping present-day biodiversity patterns of land snails and angiosperms across 53 oceanic islands from 12 archipelagos worldwide (section 1.2; Norder *et al.,* 2019). Part 1 of this thesis therefore gives insight in the dynamics of islands over the Quaternary and their imprint on modern biodiversity patterns.

In part 2 'Island Biogeography in the Anthropocene', I focus on how human activities in the past and present have shaped island ecosystems and landscapes, and compare their rate and magnitude to pre-human dynamics. I start with a case-study on a single island, Mauritius, in which I model the role of historical deforestation in shaping soil loss, and compare these rates to geological background rates. Healthy soils are a crucial component of ecosystems, and therefore form the foundation of the services that ecosystems provide to society. In this single-island case-study, I make use of the relatively well-documented history of Mauritius and trace the evolution of human-environment interactions since first human colonization (section 2.1; Norder *et al.*, 2017). Following this historical analysis of Mauritius, I present a comparative study of 30 islands in the Atlantic Ocean. In this study, I explore how differences in modern native vegetation cover across islands can be explained by contrasting societal and environmental conditions (section 2.2; Norder *et al.* in revision).

In the concluding section I will summarize the main findings of the thesis and discuss how biodiversity changes on islands over the last centuries and millennia relate to biogeographical dynamics over longer timescales. Finally, based on the findings of this thesis I will propose four research questions to guide future studies aimed at understanding how environmental and societal drivers shape island biogeographical patterns.

Figure 1. Interaction between environmental and societal conditions across spatial and temporal scales. The green part of the figure illustrate the environmental dynamics on islands over the Quaternary. Closer to the present-day, human activities (red part of figure) are added to these long-term changes. The dotted lines illustrates the permeability and variability of island boundaries (Figure modified from Norder & Rijsdijk, 2016).

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PART 1

ISLAND BIOGEOGRAPHY IN THE QUATERNARY

INTRODUCTION TO PART 1 OF THE THESIS

Over the Quaternary, the global climate alternated between cool glacials and warmer interglacials, driving large shifts in global sea level (Figure 1; Bintanja *et al.*, 2005; Bintanja & van de Wal, 2008). These glacial-interglacial cycles however, are highly asymmetrical: while glacial conditions dominate for approximately 90.000 years, the shift from glacial maxima to the next interglacial takes place in only about 10.000 years (Ruddiman, 2003). In addition, as time moves closer to the present, the amplitude of these climatic fluctuations increased (Steffen *et al.*, 2011; Zalasiewicz & Williams, 2016), resulting in the more recent glacial maxima generally being more extreme (in terms of temperature and sea level) than those closer to the beginning of the Quaternary (Figure 1).

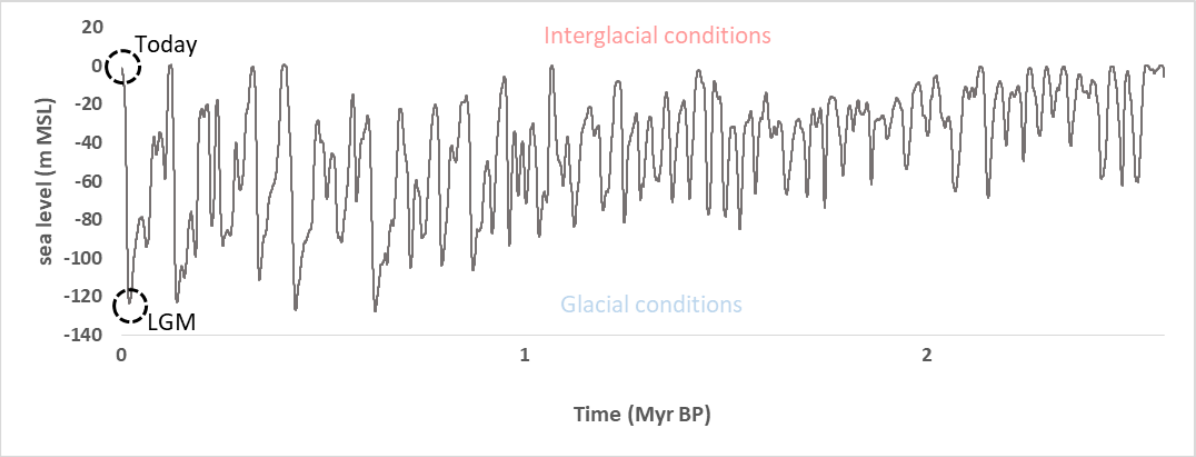

Figure 1. Sea level fluctuations over the Quaternary Period (2.588 Myr ago until today). Figure was produced based on an existing dataset of reconstructed sea levels over the last 3 Myr (Bintanja & van de Wal, 2008).

During the Last Glacial Maximum (LGM), circa 20.000 years ago, sea-levels were exceptionally low and the total area of emerged land was large (Figure 2). In those times, a person could have walked from New Guinea to Tasmania, or from Ireland to Portugal. Over subsequent millennia, temperatures and sea levels rose rapidly, eventually to reach the current high level. We are currently living in the Holocene Epoch (11.650 cal yrs BP), the most recent out of the large number of interglacials that proliferated in the Quaternary.

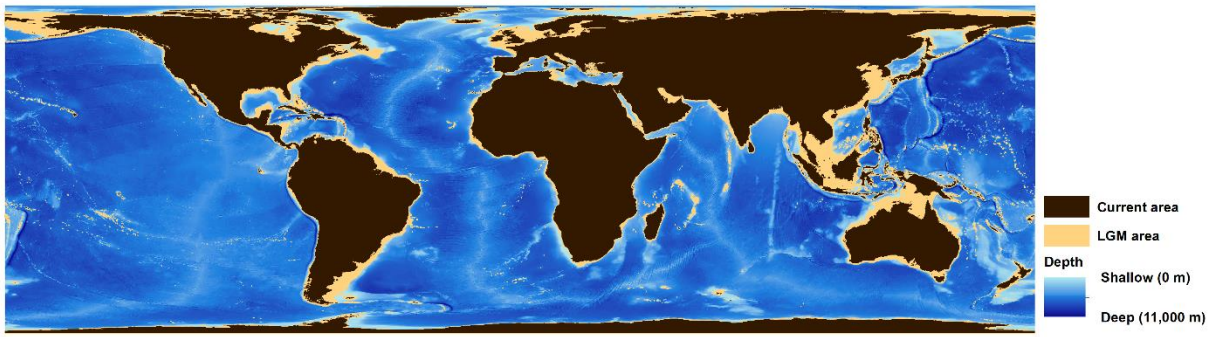

Figure 2. The land extent at the present-day high sea-level (dark shading) and at the Last Glacial Maximum (LGM) low sea-level (yellow shading) represent an extreme situation of short duration. Configurations at intermediate sea-level are more representative of glacial-interglacial cycles than the highest and lowest sea-levels.

Given their relatively small size, the proportional effect of sea level fluctuations might be particularly large on islands. In turn, sea level-driven changes in island characteristics like area and isolation have been hypothesized to affect biogeographical processes (Heaney, 1985). Some recent studies found that modern biodiversity patterns on islands show legacies of island characteristics at lower sea levels (Ali & Aitchison, 2014; Rijsdijk *et al.*, 2014; Weigelt *et al.*, 2016). However, these studies have generally focused on the exceptional and short-lasting conditions of the LGM. Given that both LGM and current interglacial situations are exceptional and short lasting, it seems relevant to explore the extent to which modern biodiversity patterns reflect past environmental conditions that are more representative of the Quaternary (Porter, 1989; Heaney *et al.*, 2013). Therefore, the main question that I will address in the first part of this thesis is:

To what extent have present-day biodiversity patterns on islands worldwide been shaped by past geographical changes?

To answer this question, we first quantified for 178 islands in 27 archipelagos worldwide how their geography changes in response to sea-level fluctuations during the last glacial-interglacial cycle (section 1.2; Norder *et al.*, 2018). This resulted in a global database of changes in archipelago configuration over the last glacial-interglacial cycle. In section 1.3 (Norder *et al.*, 2019), we use this database to statistically assess the imprint of different archipelago configurations on the modern distribution of two taxa: land snails and angiosperms.

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1.1 A global spatially explicit database of changes in island palaeo-area and archipelago configuration during the late Quaternary

Norder S.J., Baumgartner, J.B., Borges, P.A.V., Hengl, T., Kissling, W.D., van Loon, E.E., Rijsdijk, K.F. (2018). A global spatially explicit database of changes in island palaeo-area and archipelago configuration during the late Quaternary. Global Ecology and Biogeography, 27, 500–505. https://doi.org/10.1111/geb.12715

SJN coordinated the project and led the writing, SJN developed the methodology in collaboration with co-authors.

ABSTRACT

Motivation

Past sea level fluctuations have shaped island area and archipelago configuration. The availability of global high-resolution data on bathymetry and past sea levels allows reconstruction of island palaeo-geography. Studies on the role of palaeo-area often consider only the Last Glacial Maximum, which neglects the dynamics of island fusion and fission resulting from cyclic sea level fluctuations throughout the Quaternary. Currently, no global database is available to test the role of changing island geographies driven by Quaternary sea level change on evolutionary, ecological and archaeological patterns. However, data on island palaeo-environments is crucial for understanding insular biodiversity distributions and human settlement patterns. Here, we present the Palaeo-Islands and Archipelago Configuration (PIAC) database, containing sea level-driven palaeo-geography changes over the late Quaternary of 178 islands in 27 archipelagos, and discuss its relevance, limitations and uncertainties. The R functions developed to create the PIAC database are provided to allow calculations for other islands, time steps, sea-level curves and higher spatio-temporal resolutions.

Main types of variables contained

Polygon shapefiles with archipelago configuration and tables with palaeo-area per island.

Spatial location and grain

The database has a global representation, with 27 archipelagos being covered: Aldabra, Azores, Balearic Islands, California Channel Islands, Canary Islands, Cape Verde, Comoros, Cook Islands, Crozet Islands, Dutch Caribbean, Galápagos, Gulf of Guinea, Hawaii, Inner Seychelles, Juan Fernández, Kuril Islands, Madeira, Marianas, Marquesas, Mascarenes, Phoenix Islands, Pitcairn Islands, Prince Edward Islands, Revillagigedo, Samoan Islands, Society Islands and Tristan da Cunha. All data are at 1 km2 spatial resolution.

Time period and grain

The focus of this paper is on the last 35 kyr; data for the last 140 kyr are also provided. The grain is 1 kyr temporal resolution.

Level of measurement

Data are per island, grouped per archipelago.

Software format

The data were produced in the R programming language.

INTRODUCTION

Island geographies are highly dynamic. Island area, spatial location and isolation have changed drastically following geological dynamics and sea level fluctuations. These changes in palaeo-geography have shaped insular species' distributions, as well as human settlement patterns in the past. Recently developed island biogeographical models, such as the general dynamic model (GDM; Whittaker, Triantis, & Ladle, 2008; see Borregaard et al., 2017 for a review) and the glacial sensitive model (GSM; Fernández-Palacios et al., 2016) incorporate the role of long-term changes in island geography in predictions of biodiversity patterns. On time-scales of < 100 kyr, geographical changes on most oceanic islands are shaped mainly by sea level fluctuations. These fluctuations involve the repetitive fusion and fission of islands, area contraction and expansion, and changes in the number of stepping stones (reducing inter-island isolation) by the emergence and drowning of seamounts (Fernández-Palacios, 2016).

Recent findings suggest that island area and connectedness at the Last Glacial Maximum (LGM) influenced patterns of terrestrial endemic species richness on islands (Rijsdijk et al., 2014; Weigelt, Steinbauer, Cabral, & Kreft, 2016) and that sea level changes influenced the distribution of insular shallow-water marine organisms (Ávila et al., 2009; Pinheiro et al., 2017). In addition, sea level fluctuations might have influenced human population dispersal and could have modified the availability of near-shore natural resources for insular human societies (Erlandson & Fitzpatrick, 2006; Fitzpatrick & Keegan, 2007; Montenegro, Callaghan, & Fitzpatrick, 2016; Patton, 1996; van Andel, 1989). Reconstructed palaeo-shorelines have been used by several authors to understand (pre)historic patterns of human dispersal and settlement (Bailey & King, 2011; Ferentinos, Gkioni, Geraga, & Papatheodorou, 2012; Kirch, 2007; Lambeck et al., 2011). Therefore, data on the dynamics of island palaeo-environments and geographies might help to resolve key questions in island biogeography (Patiño et al., 2017) and island archaeology (Erlandson & Fitzpatrick, 2006; Montenegro et al., 2016).

Until now, temporal dynamics of palaeo-geography (e.g., the duration over which islands were connected and the rates at which island area changed) remained relatively underexplored. Biogeographical and macroecological studies so far have mainly explored the role of one (static) sea level stand, such as the current high sea level stand or the extreme low stand at the LGM, although both are highly exceptional when considering the last 1 Myr (Supporting Information Appendix S1; Bintanja, van de Wal, & Oerlemans, 2005; van Andel,

1989; Woodruff, 2010). In this paper, we present a global, spatially explicit database with a quantification of changes in island palaeo-area and reconstructions of archipelago configuration driven by sea level fluctuations during the late Quaternary. This Palaeo-Islands and Archipelago Configuration (PIAC) database consists of 178 islands located in 27 archipelagos spread around the globe (see Figure 1 for an overview). Here, we extend previous work by reconstructing island palaeo-geography dynamics on a multi-millennial time-scale and with global coverage. In the subsequent sections, we describe the methods by which the data were derived, we provide the technical validation and discuss the reliability of the database and possible applications.

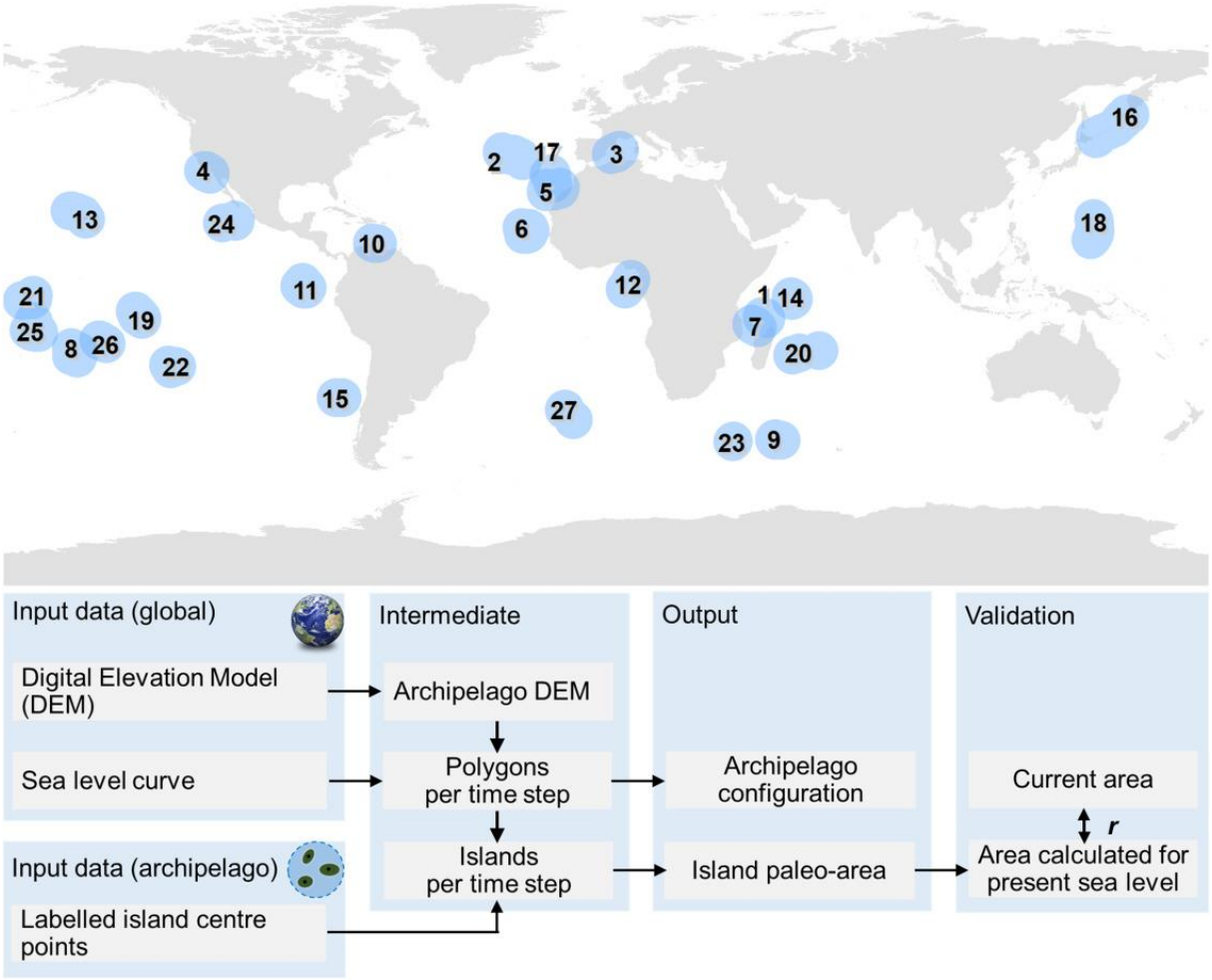

Figure 1. The top panel provides an overview of archipelagos in the PIAC database. 1 = Aldabra; 2 = Azores; 3 = Balearic Islands; 4 = California Channel Islands; 5 = Canary Islands; 6 = Cape Verde; 7 = Comoros; 8 = Cook Islands; 9 = Crozet Islands; 10 = Dutch Caribbean; 11 = Galápagos; 12 = Gulf of Guinea (São Tomé and Príncipe, Annobón); 13 = Hawaii; 14 = Inner Seychelles; 15 = Juan Fernández; 16 = Kuril Islands; 17 = Madeira; 18 = Marianas; 19 = Marquesas; 20 = Mascarenes; 21 = Phoenix Islands; 22 = Pitcairn Islands; 23 = Prince Edward Islands; 24 = Revillagigedo; 25 = Samoan Islands (Samoa and American Samoa); 26 = Society Islands; 27 = Tristan da Cunha. The lower panel shows the outline of the experimental workflow used to

generate the Palaeo Islands and Archipelago Configuration (PIAC) database. The processing steps are carried out separately for each archipelago. A global bathymetry digital elevation model and a global sea level curve are used as input data. Per 1 kyr time step, locations where the land is above sea level are delineated as polygons. The island centre points are used to identify the islands for which palaeo-area is calculated. The calculated area for the present sea level are compared with the current area by calculating the Pearson product–moment correlation coefficient (r).

METHODS

A method to calculate palaeo-area change driven by sea level fluctuations was developed by Rijsdijk, Hengl, Norder, Ávila, & Fernández-Palacios (2013) and Rijsdijk et al. (2014). To create the PIAC database, we have enhanced the method developed by Rijsdijk et al. (2013, 2014); we used higher-quality input data, the computation time is reduced, the contouring method has been improved, and the model is applied to a larger number of archipelagos (Figure 1). The workflow was subdivided into the following four steps (Figure 1): collecting input data, intermediate processing, generating output data, and data validation.

To quantify palaeo-area, three types of input data were used: The GEBCO_2014 Grid (version 20150318; www.gebco.net), which is a global 30 arc-second bathymetry digital elevation model (DEM; GEBCO, 2014); a global mean sea level curve from Lambeck, Rouby, Purcell, Sun, and Sambridge (2014) spanning 35 kyr, based on inverse modelling of c. 1,000 far-field data points and incorporating glacial isostatic adjustment (i.e., the viscoelastic response of the earth–ocean system to glacial cycles); and spatial coordinates corresponding to island centre points per archipelago. Even though sea level curves exist that span longer time-scales (e.g., Bintanja et al., 2005; Cutler et al., 2003), we used the curve from Lambeck et al. (2014) because: (a) to our knowledge, it is the most recently developed global mean sea level curve; (b) it is focused particularly on far-field locations (the vast majority of archipelagos in the data are distant from major ice-sheets); and (c) the proportional contribution of geological processes to area change and the uncertainty of sea level reconstructions increase for longer time-scales (e.g., Lambeck et al., 2014; Miller et al., 2008; Price, Clague, Bay, Road, & Landing, 2002). Even though we focused on reconstructions for a time span of 35 kyr, as an illustration of the method, data for 140 kyr based on Cutler et al. (2003) are also provided. The sea level curve was used to delimit polygons where the bathymetry DEM was above sea level at each time step. All islands that were above sea level (including presently submerged seamounts) were stored in separate polygon shapefiles per 1 kyr time step. The coordinates of island centre points were used to identify islands according

to their current names and to store their palaeo-area at each time step in a table. To assess the quality of the calculated island area, we compared the area calculated from the bathymetry DEM at the present-day sea level (0 ka) to the current area from the global database of administrative areas (GADM; www.gadm.org/version1) as reported in a dataset on present-day environmental characteristics of marine islands worldwide (Weigelt, Jetz, & Kreft, 2013). For a few islands missing from that dataset, current area was obtained from other sources. Four island pairs could not be separated at the 30 arc-second resolution, hence their area was summed in the validation data. The reconstruction of archipelago configuration and palaeo-area was carried out in R version 3.3.2 (R Core Team, 2016).

RESULTS

Description of the database

Palaeo-area and archipelago configurations were reconstructed for 178 islands within 27 archipelagos. The PIAC database is stored for a time span of 35 kyr (Lambeck et al., 2014) and 140 kyr (Cutler et al., 2003). The workflow for producing the PIAC database (R scripts and associated files) is organized within separate folders for each processing step (Figure 1): input, intermediate and output. The PIAC database and the workflow (Table 1) can be downloaded separately from ISLANDLAB (http://islandlab.uac.pt/software/ver.php?id=28) and PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.880585).

Table 1. Overview and description of files related to the Palaeo Islands and Archipelago Configuration (PIAC) database and workflow.

File name, processing step, (database/workflow)	File format	Description (and source)
archipelago_shp$_{OUT}^{(DB)}$	Folder with ESRI polygon shapefiles (.shp)	Archipelago configuration and island shorelines with polygons for each present-day island that was above sea level for each 1 kyr time step
area_archipelago$_{OUT}^{(DB)}$	CSV and XLSX	Palaeo-area (km^2) for each 1 kyr time step for islands within an archipelago
area_global$_{OUT}^{(DB)}$	CSV and XLSX	Palaeo-area (km^2) for each 1 kyr time step for all islands in the database
archipelagoDEMsin$_{INTER}^{(WF)}$	GeoTIFF (.tif)	Bathymetry digital elevation model (DEM) for each archipelago
archipelago_pnt$_{IN}^{(WF)}$	KML	Centre points of islands within an archipelago
GEBCO_2014_1D$_{IN}^{(WF)}$	netCDF	Global digital elevation model (including bathymetry) from the GEBCO_2014 Grid, version 20150318, www.gebco.net. The file can be downloaded from https://www.gebco.net/data_and_products/gridded_bathymetry_data/
time_level_Lambeck$_{IN}^{(WF)}$ time_level_Cutler$_{IN}^{(WF)}$	Serialized R object (.rds)	Global mean sea level curves (metres relative to present sea level) from Lambeck et al. (2014) and Cutler et al. (2003)
PIAC_run$^{(WF)}$	R script	Workflow for preparing the data
PIAC_functions$^{(WF)}$	R script	Functions for preparing the data

Note. The PIAC database $^{(DB)}$ is available for 1 kyr time steps over periods of 35 and 140 kyr (created data are in the World Sinusoidal projection, EPSG code: 54008). For each of the files contained in the PIAC database $^{(DB)}$ and workflow $^{(WF)}$, the processing step ($_{IN}$, $_{INTER}$ or $_{OUT}$) is indicated and a file description provided.

In Figure 2, the data on archipelago configuration and palaeo-area are visualized for the Canary Islands. As a result of bathymetric differences, each island shows a unique area change signature. Similar graphs of palaeo-area change for other archipelagos are presented in Supporting Information Appendix S2 for a time span of 35 kyr (Lambeck et al., 2014) and 140 kyr (Cutler et al., 2003).

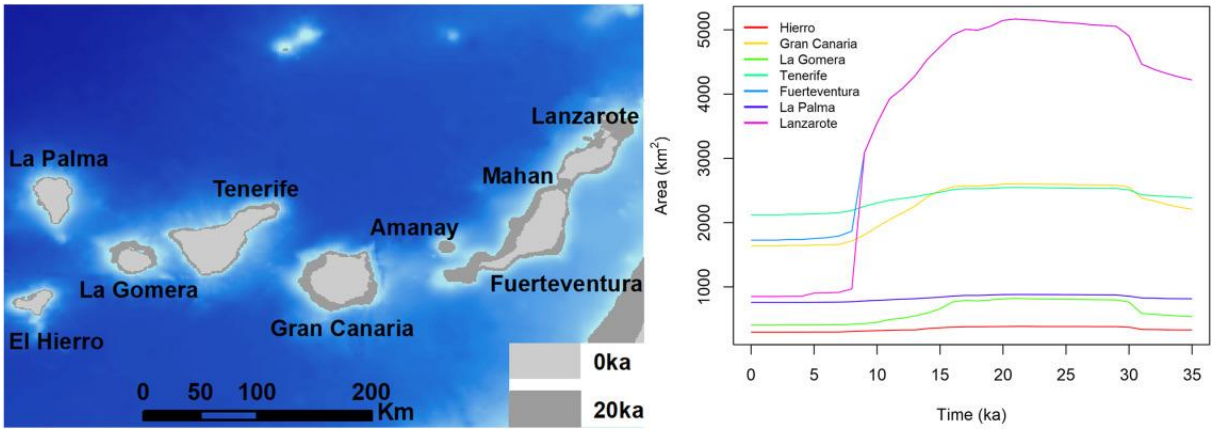

Figure 2. Changes in palaeo-area within the Canary Islands. The map on the left shows the archipelago configuration at 20 ka (dark grey), with the present archipelago configuration added as a reference (light grey). The right panel shows the reconstructed palaeo-area changes (in square kilometres) for the seven major islands of this archipelago over a period of 35 kyr. The figure was created by using the sea level curve from Lambeck et al. (2014).

Validation

The comparison of the area calculated at the present-day sea level with the real current island area indicates that they are highly correlated (Pearson product–moment correlation coefficient, r = 0.99; Supporting Information Appendix S3). For most islands, the calculated area is slightly larger than the real area, but in a few cases it is smaller. The deviations stem from the spatial resolution (30 arc-second) of the bathymetry DEM. Consequently, the proportional deviations are larger for small islands (Supporting Information Appendix S3).

DISCUSSION

Accuracy

Possible inaccuracies in the calculated palaeo-area and reconstructed archipelago configuration stem from two factors. The first factor is the resolution of the bathymetry DEM (30 arc-second; c. 1 km at sea level at the equator). To our knowledge, there is no publicly available global bathymetry DEM with a higher resolution than the one used to produce this database. As DEMs with higher resolution become available, the code accompanying this paper can be applied to generate outputs with increased accuracy. Second, we used a global mean sea level curve for reconstructing regional geographies. Sea level is not uniform across the globe; regional deviations are caused by the complex interactions between oceans, ice-sheets and the Earth's crust, including geological processes (e.g., glacial isostatic adjustment, and vertical land movement resulting from both gradual and sudden tectonic processes), variations in ocean mass and density, and ‘fingerprint’ effects, such as the gravitational attraction between water and ice-sheets (Clark, Farrell, & Peltier, 1978; Farrell & Clark, 1976; Kopp, Hay, Little, & Mitrovica, 2015; Lambeck et al., 2014; Milne & Mitrovica, 2008; Raymo, Mitrovica, Leary, Deconto, & Hearty, 2011). Although these different processes might negate each other, regional deviations from the global sea level curve up to tens of metres are possible (Kopp et al., 2015; Milne & Mitrovica, 2008; Woodroffe, McGregor, Lambeck, Smithers, & Fink, 2012). Given that the sea level curve from Lambeck et al. (2014) was developed for far-field regions (regions far from former ice-sheets), our reconstructions of palaeo-area and archipelago configuration for islands located in or close to tropical regions are likely to have the highest accuracy. Whether or not the inaccuracies stemming from the factors outlined above are relevant for specific archipelagos should be decided based on the spatio-temporal scale and scope of the project. Although some studies have reconstructed changing island geographies resulting from both geological processes and sea level

fluctuations for specific archipelagos over time-scales of several 100 kyr (e.g., Ali & Aitchison, 2014; Price & Elliott-Fisk, 2004), making such detailed reconstructions over long time-scales is currently unfeasible for many archipelagos owing to lack of data, and is therefore currently impossible on a global scale.

Applications

The global PIAC database enables movement beyond a focus on extreme archipelago configurations, such as during the present interglacial high or the LGM (see Ferentinos et al., 2012; Voris, 2000; Warren, Strasberg, Bruggemann, Prys-Jones, & Thébaud, 2010 for examples using multiple time steps). The database permits assessment of the potential for vicariance events and stepping stone dispersal in evolutionary and biogeographical studies (see Fordham et al., 2017, who provide a similar line of argumentation for palaeo-climate). For instance, the database might facilitate answering questions such as: what is the influence of repetitive fusion and fission of palaeo-islands (such as Mahan into Fuerteventura and Lanzarote; Figure 2) on biodiversity and phylogenetic patterns? And, is present-day beta diversity related to inter-island palaeo-distance? The database also allows for the reconstruction of coastal environments for archaeological studies, exploration of potential archaeological sites in currently submerged regions (Erlandson & Fitzpatrick, 2006; Lambeck & Chappell, 2001; Rick, Kirch, Erlandson, & Fitzpatrick, 2013), and the development of simulation models in human dispersal studies (Ferentinos et al., 2012; Montenegro et al., 2016).

Area or isolation metrics derived from the PIAC database can be used as explanatory variables in macroecological and evolutionary studies. Examples of metrics that could be calculated from the database are as follows: rate of area change; minimal, maximal or average area over a biogeographically relevant time period; or the mean, minimal and maximal inter-island distance. For local scale biogeographical, phylogenetic, population genetic and archaeological studies, we recommend use of a regional sea level curve where available (Simaiakis et al., 2017; van Andel, 1989; Warren et al., 2010). In addition, regional crustal tectonic or other effects leading to temporal deviations from the global mean curve are not incorporated. If precise timings of geographical change are required, reference to known local deviations from the global mean sea level curve is recommended. The database presented in this paper should be regarded as an approximation of palaeo-area and archipelago configuration shaped by sea level fluctuations to be refined as new data and methods become

available. The R scripts and functions included in the database allow more detailed calculations for specific islands or archipelagos where a regional sea level curve or a high-resolution bathymetry DEM exists.

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1.2 Beyond the Last Glacial Maximum: island endemism is best explained by long-lasting archipelago configurations

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SJN coordinated the project, largely conceived and designed the study, analysed the data and wrote the manuscript. Co-authors contributed data, revised the manuscript and participated actively in discussions about interpretation of the results.

ABSTRACT

Aim

To quantify the influence of past archipelago configuration on present-day insular biodiversity patterns, and to compare the role of long-lasting archipelago configurations over the Pleistocene to configurations of short duration such as at the Last Glacial Maximum (LGM) and the present-day.

Location

53 volcanic oceanic islands from 12 archipelagos worldwide—Azores, Canary Islands, Cook Islands, Galápagos, Gulf of Guinea, Hawaii, Madeira, Mascarenes, Pitcairn, Revillagigedo, Samoan Islands and Tristan da Cunha.

Time period

The last 800 kyr, representing the nine most recent glacial–interglacial cycles.

Major taxa studied

Land snails and angiosperms.

Methods

Species richness data for land snails and angiosperms were compiled from existing literature and species checklists. We reconstructed archipelago configurations at the following sea levels: the present-day high interglacial sea level, the intermediate sea levels that are representative of the Pleistocene and the low sea levels of the LGM. We fitted two alternative linear mixed models for each archipelago configuration using the number of single-island endemic, multiple-island endemic and (non-endemic) native species as a response. Model performance was assessed based on the goodness-of-fit of the full model, the variance explained by archipelago configuration and model parsimony.

Results

Single-island endemic richness in both taxonomic groups was best explained by intermediate palaeo-configuration (positively by area change, and negatively by palaeo-connectedness), whereas non-endemic native species richness was poorly explained by palaeo-configuration.

Single-island endemic richness was better explained by intermediate archipelago configurations than by the archipelago configurations of the LGM or present-day.

Main conclusions

Archipelago configurations at intermediate sea levels—which are representative of the Pleistocene—have left a stronger imprint on single-island endemic richness patterns on volcanic oceanic islands than extreme archipelago configurations that persisted for only a few thousand years (such as the LGM). In understanding ecological and evolutionary dynamics of insular biota it is essential to consider longer-lasting environmental conditions, rather than extreme situations alone.

INTRODUCTION

Oceanic islands are among the most dynamic systems in the world: they emerge and submerge; they shrink and expand; and they split and merge. Changes in island geography and archipelago configuration are shaped by geological processes (e.g., plate tectonics, island ontogeny and within-island volcanism) and sea-level fluctuations (Fernández-Palacios et al., 2016). These sea-level fluctuations, driven by glacial–interglacial cycles over the Pleistocene, have influenced all archipelagos and their constituent islands simultaneously. During glacial periods, sea levels were low and archipelago configurations were often very different: islands had larger surface areas than at present, with some islands fused into larger islands. For example, the Hawaiian islands of Maui, Molokai and Lanai have repeatedly merged to form a single landmass (the Maui Nui complex; Price, 2004). Islands were also less isolated, with their larger areas reducing inter-island distance and with emerging sea mounts forming stepping stones for dispersal (Ali & Aitchison, 2014; Pinheiro et al., 2017; Rijsdijk et al., 2014). In contrast to these glacial periods, during interglacial high sea-level stands islands were smaller and further apart, as some islands were submerged and palaeo-islands fragmented. Glacial–interglacial cycles have followed a recurrent pattern over the Pleistocene with glacial periods spanning a much longer duration than interglacials (Figure 1). Therefore, for most of the Pleistocene, sea levels were lower than today, corresponding to larger and less isolated islands.

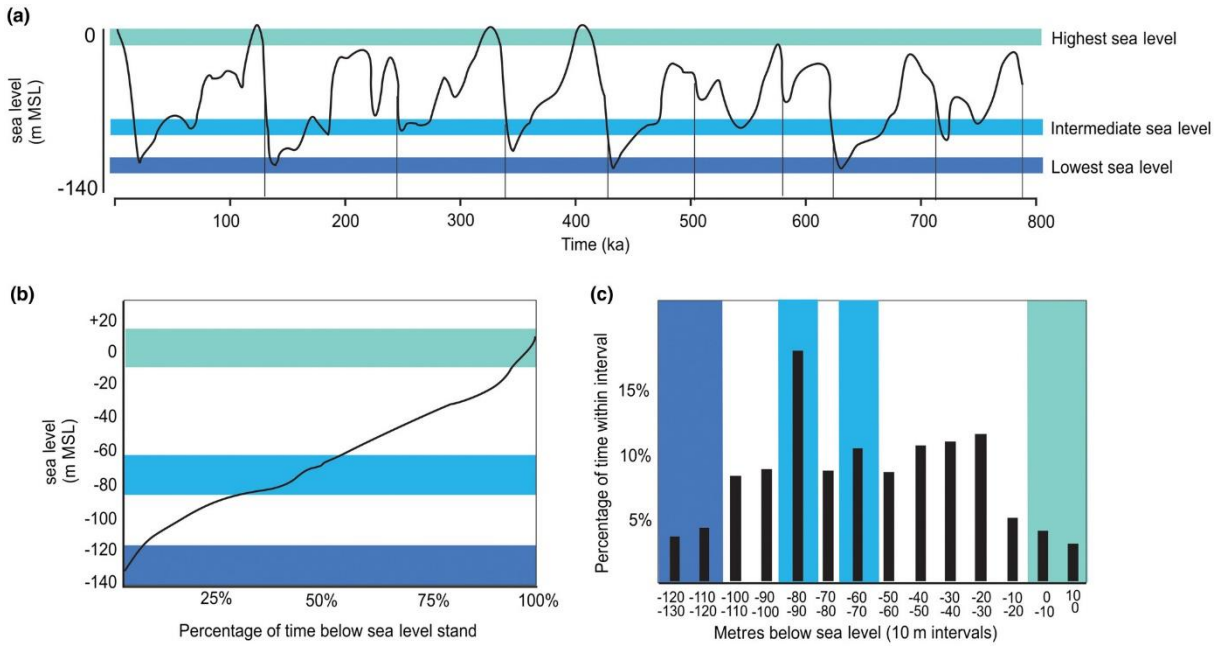

Figure 1. Characterization of sea-level fluctuations over the last ~800 kyr at highest, intermediate and lowest sea levels. (a) Sea-level fluctuations over the nine most recent glacial–interglacial cycles covering the period of

the last ~800 kyr. (b) The percentage of time over the last ~800 kyr that the sea level was below a certain sea level. (c) The most frequently occurring sea levels are quantified as the percentage of time over the last ~800 kyr that sea levels were within a certain interval [in 10-m bins, e.g., between −90 m mean sea level (MSL) and −80 m MSL]. The period of ~800 kyr was chosen because it spans nine full glacial–interglacial cycles (estimated duration of interglacials from Tzedakis et al., 2012). All figures are based on data from Bintanja et al. (2005).

It has long been suggested that past archipelago configurations during lower sea levels have influenced the distribution and evolution of insular biota (Heaney, 1985; Mayr, 1944). Recently, attempts have been made to quantify this relationship (Ali & Aitchison, 2014; Fernández-Palacios, 2016; Heaney, Walsh, & Peterson, 2005; Papadopoulou & Knowles, 2017; Rijsdijk, Hengl, Norder, Ávila, & Fernández-Palacios, 2013; Rijsdijk et al., 2014; Weigelt, Steinbauer, Cabral, & Kreft, 2016). However, as Heaney, Balete, and Rickart (2013) noted, emphasis has been on the relatively short-lasting configuration prevailing during the Last Glacial Maximum (LGM) (e.g., Weigelt et al., 2016). The LGM refers to an exceptional and extreme situation (at approximately 21 ka) of maximum sea-level fall within only the most recent glacial–interglacial cycle of the nine cycles occurring over the last 800 kyr. Even when summing up the duration of all glacial maxima over the last 800 kyr, together they would constitute only about 2% of the time elapsed (Figure 1). The duration of these glacial maxima may have been insufficient to shape the assembly of island biotas and especially their endemic component. Similarly, Porter (1989) asked whether short-lasting extremes such as the LGM and the current interglacial might have received undue attention, and recognized the important role of average Quaternary conditions in landscape evolution and geomorphology. The cyclic nature of Pleistocene sea-level fluctuations leads to alternating periods of island separation and connection, and of shrinking and expanding island areas. Some of these periods lasted longer than others, and some sea-level stands occurred repeatedly, while others were more exceptional (Figure 1). Although Porter (1989) suggested the potential relevance of intermediate Pleistocene conditions for understanding biogeographical patterns, we are unaware of any study so far that has quantitatively analysed their relationship. Given that both LGM and current interglacial situations are exceptional and short lasting, it seems important to explore the extent to which present-day distributions of insular biota reflect past environmental conditions that are more representative of the Pleistocene.

Climatic and environmental fluctuations over the Pleistocene affected the extinction, speciation, fragmentation, merging and population size of biota (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Dynesius & Jansson, 2002; Hofreiter & Stewart, 2009). However, the rates of biogeographical processes shaping island biota during Pleistocene climatic fluctuations

varied over time and across taxa (Knowles, 2001a, 2001b; Shepard & Burbrink, 2009; Willis & Niklas, 2004). To complicate matters further, the patterns of island endemism that we observe today might have been shaped by past biotic and abiotic regimes that are difficult to distinguish in retrospect (Figure 2). Despite the difficulty in making generalized statements about the prime response of biota to glacial–interglacial cycles, it is unambiguous that present-day biota consist of a large proportion of species (native and endemic) that have survived several glacial and interglacial periods (Hewitt, 2000; Webb & Bartlein, 1992). Present-day insular species richness might therefore be considered to be the cumulative outcome of varying biogeographical processes operating during different periods in the past (cf. Waldron, 2010; Dynesius & Jansson, 2014).

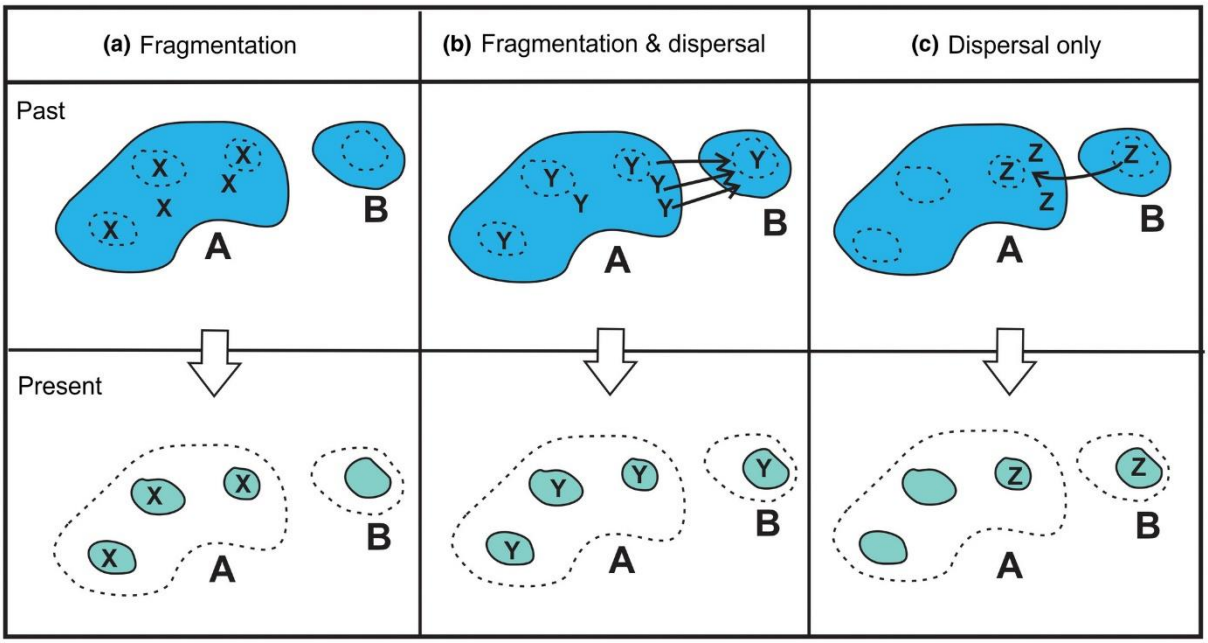

Figure 2. Conceptual figure illustrating how observed present-day endemism patterns might result from fragmentation and/or dispersal. The chorotype of a species might change from single-island endemic (SIE) to multiple-island endemic (MIE) as a result of either of these processes (or a combination thereof). (a) SIE on palaeo-island A becomes MIE by fragmentation. (b) MIE shared by palaeo-islands A and B continues to be a MIE (but as a result of fragmentation and dispersal). (c) SIE on palaeo-island B becomes MIE by dispersal.

Volcanic oceanic islands are isolated from continental landmasses and therefore receive few colonists. The corresponding low rate of genetic exchange results in a relatively large number of endemic species confined to a single island (single-island endemics, SIE), or to several islands within the same archipelago (multiple-island endemics, MIE). This contrasts with (non-endemic) native species (N), which also occur outside the archipelago. There are two reasons to suggest that the effect of palaeo-configuration on extant species will be stronger for endemics (especially SIE) than natives (N). First, endemics differ from natives (non-endemic)

in their adaptation to the insular environment and archipelagic setting; endemic species have frequently undergone a longer duration of in situ insular evolution (Warren et al., 2015; Whittaker & Fernández-Palacios, 2007; Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017) than non-endemic natives (N) and have therefore experienced glacial–interglacial cycles for a longer period (in the case of palaeo-endemics insular evolution was not the only process, but the idea of experiencing glacial–interglacial cycles for longer periods still applies). Second, taxa frequently exhibit high levels of endemism as a consequence of low levels of gene flow with neighbouring landmasses (Kisel & Barraclough, 2010). Further, low gene flow is often a consequence of a low dispersal capacity. Such poor-dispersing taxa may be expected to be impacted more profoundly by changes in the geographical configuration of archipelagos than good dispersers (cf. Borges & Hortal, 2009). Such enhanced impact is due to the lower chances of successful colonization of another island and the narrower habitat availability within their dispersal range. However, the degree to which archipelago configuration influences patterns of endemic species richness probably differs among taxa [e.g., resulting from differences in dispersal capabilities (Claramunt, Derryberry, Remsen, & Brumfield, 2012), number of life cycles (Comes & Kadereit, 1998), population sizes and ecological requirements]. Because of their isolated nature and high levels of endemism, volcanic oceanic islands are excellent study systems for understanding the role of long-term geographical processes on speciation and species richness, such as glacial–interglacial changes in archipelago configuration (Warren et al., 2015).

Here, we explore to what extent the persistence and recurrence of different archipelago configurations have left an imprint on present-day species richness on oceanic islands of volcanic origin. Archipelago configuration refers to any combination of area and connectedness (or its antonym: isolation) of islands within the same archipelago (palaeo-configuration refers to an archipelago configuration in the past). We focus here exclusively on changes in archipelago configuration driven by sea-level fluctuations, which have affected all islands globally (Norder et al., 2018). Although island bathymetry is also shaped by geological processes (such as volcanic eruptions, uplift, subsidence and erosion), these are not the main focus of our analysis because they are highly island and archipelago specific (Triantis, Whittaker, Fernandez-Palacios, & Geist, 2016; Whittaker, Triantis, & Ladle, 2008). We restrict the analysis to volcanic oceanic islands to avoid the confounding effect of different abiotic conditions and archipelago configuration dynamics among other island types, such as archipelagos of atolls, land-bridge continental shelf islands and continental fragments

(Ali, 2017; Fernández-Palacios et al., 2016; Warren, Strasberg, Bruggemann, Prys-Jones, & Thébaud, 2010; Whittaker & Fernández-Palacios, 2007). We focus on two contrasting taxa with generally good availability of data, land snails and angiosperms, because they differ in terms of dispersal capabilities, ecological requirements and endemism level (which, on volcanic oceanic islands, is much higher for land snails than for angiosperms; Groombridge, 1992; Whittaker & Fernández-Palacios, 2007). Specifically, we test three hypotheses, that: (a) the signal of palaeo-configuration is stronger for SIE than for those that have wider distributions (i.e., MIE and N); (b) for SIE, palaeo-configurations that are more representative of the Pleistocene, associated with intermediate sea levels, will have left a stronger signal than extreme configurations of a short duration (such as the LGM); and (c) land snails will be more affected by past archipelago configurations than angiosperms because they have more restricted distributions and often have lower dispersal capabilities. We test all hypotheses against the classical expectation that present-day richness is best explained by current archipelago configuration.

MATERIALS AND METHODS

Islands and archipelagos

In total, 53 volcanic oceanic islands representing 12 archipelagos (Azores, Canary Islands, Cook Islands, Galápagos, Gulf of Guinea, Hawaii, Madeira, Mascarenes, Pitcairn, Revillagigedo, Samoan Islands and Tristan da Cunha) were included. Our criteria for inclusion of an island were: (a) species data were available for both land snails and angiosperms; (b) islands are oceanic and of volcanic origin.

Species richness data

Species richness data for land snails for each island of the dataset were compiled from existing literature and species checklists (references in Supporting Information Table S1). Infraspecific entities were grouped into their respective specific taxonomic rank. Species status was standardized based on MolluscaBase (2017; https://www.molluscabase.org). We considered only islands for which complete lists were available. Recorded extinct species were included in the dataset, while species presumed to be introduced were excluded (Cameron et al., 2013; Triantis, Rigal, et al., 2016). Land snails were classified according to chorotype (a group of species with their distribution restricted to a certain region; see Table 1

for an overview of chorotype acronyms) as: native non-endemic (N_S), multiple-island endemic (MIE_S) and single-island endemic (SIE_S).

Table 1. Description and sources of the chorotypes and archipelago configurations (palaeo-configurations and present-day configurations) used in this study.

Acronym	Group	Description	Sources
Chorotypes			
SIE_S	Land snails	Single-island endemic species richness	Supporting Information Table S1
SIE_P	Angiosperms	Single-island endemic species richness	Weigelt et al. (2016)
N_S	Land snails	Native (non-endemic) species richness	Supporting Information Table S1
N_P	Angiosperms	Native (non-endemic) species richness	Weigelt et al. (2016)
MIE_S	Land snails	Multiple-island endemic species richness	Supporting Information Table S1
Archipelago configurations			
SLH_{CA}	Highest	Archipelago configuration model based on the present-day sea level, consisting of only current area (CA)	(GADM; http://www.gadm.org/version1)
SLH_{CACI}	Highest	Archipelago configuration model based on the present-day sea level, consisting of CA and current isolation (CI)	(GADM; http://www.gadm.org/version1)
SLI_{MED}	Intermediate	Archipelago configuration model based on the median sea level of −65 m mean sea level (MSL), consisting of CA, delta area (dA) and palaeo-connectedness (PC)	Norder et al. (2018)
SLI_{FREQ}	Intermediate	Archipelago configuration model based on the central value of the most frequently occurring sea-level interval of −85 m MSL, consisting of CA, dA and PC	Norder et al. (2018)
SLL_{GM}	Lowest	Archipelago configuration model based on the Last Glacial Maximum sea level of −134 m MSL, consisting of CA, dA and PC	Lambeck et al. (2014), Norder et al. (2018)
SLL_{-122}	Lowest	Archipelago configuration model based on the sea level −122 m MSL, consisting of CA, dA and PC	Weigelt et al. (2016)

Angiosperm richness data were obtained from Weigelt et al. (2016) for native non-endemics (N_P) and single-island endemics (SIE_P). Weigelt et al. (2016) also included angiosperm species endemic to past island units at a sea level of −122 m (PIE_P). In a similar way, land snail species endemic to past island units (PIE_S) at various sea levels (see below) were initially calculated. However, for both land snails and angiosperms, the correlation between SIE and palaeo-island endemics (PIE) was $r > 0.99$, suggesting that for oceanic islands of volcanic origin, this distinction does not provide additional insights (Supporting Information Tables S2 and S3). Therefore, we only consider present-day chorotypes (i.e., N, MIE and SIE classes, but not PIE) for further analysis.

Palaeo-configuration data

We considered three archipelago configurations (Figure 3; Table 1): (a) current configuration at the present-day high interglacial sea level (hereafter: “highest”) with small island area and

small connectedness (i.e., large isolation); (b) palaeo-configuration at intermediate sea levels (hereafter: "intermediate") with intermediate island area and connectedness; (c) palaeo-configuration at minimum sea level (hereafter: "lowest") with largest island area and largest connectedness.

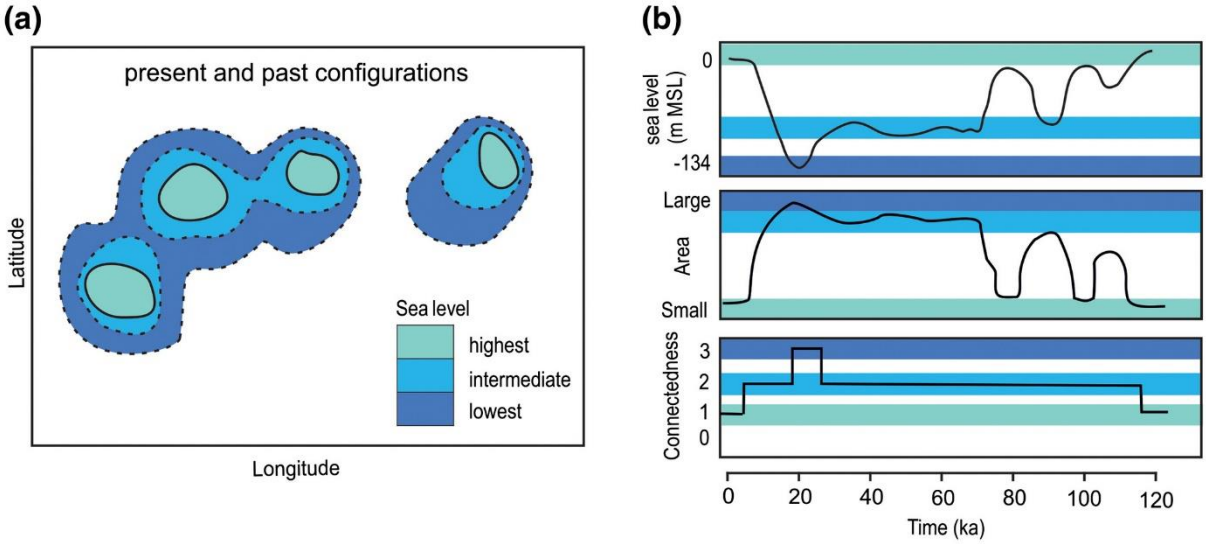

Figure 3. Conceptual figure showing three archipelago configurations (highest, intermediate and lowest sea level) that were used in this study, illustrated for one hypothetical sea-level cycle. (a) Conceptual illustration of how sea-level change affects archipelago configuration. (b) The three panels show how sea level (top), area (middle) and connectedness (bottom) change for one specific island. Connectedness is quantified as the number of present-day islands connected in a palaeo-island. Archipelago configurations at intermediate sea level are more representative of this cycle than the highest and lowest sea levels, which both represent an extreme configuration of short duration.

To represent long-term palaeo-configuration at intermediate sea levels (SLI), we calculated two alternative summary measures: SLI_{FREQ} for the most recurrent, and SLI_{MED} for the most persistent sea level. Both were calculated for the last nine full glacial–interglacial cycles using the estimated duration of interglacials from Tzedakis, Channell, Hodell, Kleiven, and Skinner (2012) and sea-level data from Bintanja, van de Wal, and Oerlemans (2005). Over these nine glacial–interglacial cycles (between 787.9 and 11.2 ka), sea levels between −90 m mean sea level (MSL) and −80 m MSL occurred most frequently (16% of the time sea levels were within this interval; Figure 1). We used the central value (−85 m) of this interval to represent the most frequent long-term sea level stand (SLI_{FREQ}). For 32.5% of the time, MSL was below −85 m MSL. Over the same nine glacial–interglacial cycles, the median sea level (SLI_{MED}) was −65 m MSL (the mean is −64 m MSL). For 50% of the time, MSL was below −65 m; for 9.5% of the time sea levels were between −70 and −60 m MSL (Figure 1). To reconstruct palaeo-configuration during the lowest sea levels (SLL) we used two sea-level stands: (a) the

most recent estimate for the LGM low stand (SLL_{GM}) of −134 m MSL (Lambeck, Rouby, Purcell, Sun, & Sambridge, 2014); and (b) the sea-level low stand of −122 m MSL (SLL_{-122}) selected by Weigelt et al. (2016). To represent archipelago configuration at highest sea levels (SLH), we used the present-day sea level (although for 1.5% of the last ~800 kyr sea levels were higher; Figure 1).

We obtained the palaeo-configuration of all islands at the respective sea level stands (SLI_{MED}, SLI_{FREQ}, SLL_{-122} and SLL_{GM}) from the Palaeo-Islands and Archipelago Configuration (PIAC) database (Norder et al., 2018). For each palaeo-configuration, we calculated delta area (dA; km2) per reference sea level as the log-transformed absolute difference between current area and palaeo-area. Palaeo-connectedness (PC) was calculated for each respective sea level stand as the number of present-day islands that were connected within a single palaeo-island at a lower sea level. For the highest sea level we used the current area (CA) from the Database of Global Administrative Areas (GADM; https://www.gadm.org/version1), as reported in Weigelt et al. (2016). Current isolation (CI) was calculated as the distance to the nearest other island for which species data were available. As island age is known to influence endemism patterns on individual islands and archipelagos (Peck, 1990; Whittaker et al., 2008), we tested for correlation (herein Pearson's correlation) between each of the aforementioned archipelago configuration variables and island age (island ages and sources in Supporting Information Table S4). All correlations were low and non-significant (Supporting Information Table S5 and Figure S1a–h). This is unsurprising; although volcanic and erosional processes show some age-progressive trends (Whittaker et al., 2008), it is problematic to stereotype the consequences of such trends for area and connectivity through sea-level fluctuations. The aim of the current study is to assess biotic responses to sea level driven changes in archipelago configuration, which is a necessary in-between step towards an integrated understanding of the role of archipelago dynamics and complex island geologies in shaping island biodiversity (Borregaard et al., 2017).

Statistical analyses

All the statistical analyses conducted in this study were implemented within the R statistical programming environment (R Core Team, 2016). To test our first hypothesis ("H1: palaeo-configuration per chorotype")—that the role of palaeo-configuration is stronger for SIE than for MIE and N—we fitted linear mixed models separately for each chorotype. In each model, we used archipelago identity as a random effect (Bunnefeld & Phillimore, 2012; Cameron et

al., 2013) and used a Poisson error structure. Each of the models for palaeo-configuration consisted of the following fixed effects: current area (CA), delta area (dA) and palaeo-connectedness (PC) at either intermediate or lowest sea levels. We adopted linear mixed models with archipelago identity as random effect to account for non-independence of data due to the underlying archipelagic structure (Borregaard et al., 2017; Bunnefeld & Phillimore, 2012; Triantis, Economo, Guilhaumon, & Ricklefs, 2015). For example, subsidence rates and erosion regimes (which are mainly climate-driven) vary greatly between archipelagos (Triantis, Whittaker, et al., 2016). We fitted the models with the lmerTest R package, which is a wrapper around lme4 (Bates, Mächler, Bolker, & Walker, 2015).

To test our second hypothesis ("H2: intermediate configuration and SIE")—that the role of intermediate palaeo-configurations on SIE is stronger than extreme configurations—we included six alternative archipelago configuration models, including two for each of the three sea levels considered (lowest, intermediate, highest; Figure 3). For the intermediate, most representative, sea level we fitted separate models for the median and most frequent sea levels (SLI_{MED}, SLI_{FREQ}). For the lowest sea level (corresponding to extreme configurations of short duration) we fitted separate models for −134 m MSL (SLL_{GM}, Lambeck et al., 2014) and a sea level of −122 m MSL (SLL_{-122}, Weigelt et al., 2016). In addition to the models for intermediate and lowest sea levels, we included two models for the present-day high sea level. The first model (SLH_{CA}) consists of current island area (CA) as the only fixed effect. The second model (SLH_{CACI}) consisted of two fixed effects: CA and current isolation (CI). We have included this alternative model because those islands with large PC might also be more proximate today.

To test our third hypothesis ("H3: palaeo-configuration per taxon")—that land snails are more affected by palaeo-configuration than angiosperms—we fitted the six models (SLH_{CA}, SLH_{CACI}, SLI_{MED}, SLI_{FREQ}, SLL_{GM}, SLL_{-122}) for each chorotype of land snails (N_S, MIE_S, and SIE_S) and angiosperms (N_P, SIE_P).

To make an informed decision about which archipelago configurations were most relevant in ecological terms, we adopted two complementary approaches to indicate which configuration had strongest statistical support: (a) we assessed for each model the total variance explained, and the proportion of variance explained by archipelago configuration; (b) we ranked significant models based on Akaike's information criterion corrected for sample size (AICc). For the first approach, we calculated the marginal and conditional R^2 (Nakagawa &

Schielzeth, 2013) for each model per chorotype. We choose these metrics because they are appropriate within a linear mixed model framework (Nakagawa & Schielzeth, 2013). The conditional R-squared (R^2_C) provides a measure of the variance explained by the full model (fixed and random effects). The marginal R-squared (R^2_M) indicates the variance explained by archipelago configuration (fixed effects). The difference between R^2_M and R^2_C was calculated to reflect the variance explained by archipelago identity (see Ibanez et al., 2018 for a similar approach). For the second approach, we started by selecting those models for which all individual predictors were significant at $p < 0.05$ to arrive at a set of "suggestive, but inconclusive" models (Murtaugh, 2014). The remaining models were ranked based on AICc. Although a cut-off rule of Δ AIC > 2 relative to the best model is often used, it is an arbitrary rule and models with a Δ AICc value between 2 and 7 should not be neglected (Burnham, Anderson, & Huyvaert, 2011). It should be noted that AICc is not an absolute measure of fit (Symonds & Moussalli, 2011) but is a metric that balances model complexity and model fit (Mundry, 2011). Therefore, Burnham et al. (2011) recommend inclusion of a metric to quantify how well models perform (we choose R^2_C and R^2_M). To summarize, we calculated R^2_C to assess goodness-of-fit of the full model, R^2_M to assess the variance explained by archipelago configuration and Δ AICc to assess model parsimony.

RESULTS

Description of the data

While all islands were larger than today during lowest and intermediate sea levels, each island has a unique area change pattern in response to sea level fluctuations (Supporting Information Figure S2a–c). Consider, for example, these four islands, which today have a similar area of roughly 140 km^2: Socorro (Revillagigedo), Flores (Azores), Tutuila (Samoan Islands) and Príncipe (Gulf of Guinea). At SLI_{MED} their sizes were respectively 179%, 154%, 224% and 516% of the present day. At SL_{LGM}, the respective values were 219%, 240%, 308% and 951% (cf. Norder et al., 2018). Also PC responded very differently across islands following the same amount of sea-level change. At the median and most frequent sea levels (SLI_{MED}, SLI_{FREQ}) seven and eight of the 53 present-day islands were connected to another island within their archipelago, respectively. At a sea level of −122 m MSL (SLL_{-122}) and during the LGM (SLL_{GM}), 12 and 13 islands were connected, respectively. Pearson's correlations of the predictor variables PC and palaeo-area range from r = 0.28 to r = 0.55, with the highest values for palaeo-area and PC at the same sea-level stand (Supporting Information Table S6). PC

values at different sea levels are strongly correlated, with lowest correlations between SLI_{MED} and SLL_{GM} (r = 0.67) and highest correlations between SLL_{-122} and SLL_{GM} (r = 0.97). The correlations between palaeo-area at different sea levels show the same pattern: palaeo-areas at SLI_{MED} and SLL_{GM} are least correlated (r = 0.87), while the palaeo-areas at SLL_{GM} and SLL_{-122} can be considered identical (r > 0.99) for our dataset of 53 volcanic oceanic islands.

For land snails, our data represented 1,903 species, consisting of 1,430 SIES, 302 MIE_S and 171 native species N_S. In total, 1,627 SIE_P were included in our dataset. Native species richness for angiosperms could not be calculated from the available data because we only had data on species richness per island but no species identities (see Weigelt et al., 2016). For land snails, the mean proportion of each chorotype across islands was 28.7% for N_S, 34% for MIE_S and 37.2% for SIE_S. Mean inter-island chorotype proportion for angiosperms was 92.9% for N_P and 7.1% for SIE_P.

The role of archipelago configuration differs between chorotypes and taxa

We found that the variance in species richness that was explained by palaeo-configuration was larger for SIE than for species with a wider distribution, supporting H1 (palaeo-configuration per chorotype). The variance explained by palaeo-configuration (R^2_M of SLL_{GM}, SLL_{-122}, SLI_{FREQ}, SLI_{MED}) was 30%–47% for SIE_S and 33%–41% for SIE_P (Figure 4). For the more widespread chorotypes, the corresponding values were generally much lower: only 2%–3% for N_S, 13%–20% for MIE_S and 22%–27% for N_P. Comparing models in terms of AICc revealed a similar pattern. For SIE_S and SIE_P some palaeo-configuration models were within Δ AICc < 7, while for MIE_S, N_S and N_P, there were no significant palaeo-configuration models within this range. These p-values were rather unrestrictive because consistent overdispersion was present across models. As a result, the subset of significant models initially included before AICc ranking was relatively broad.

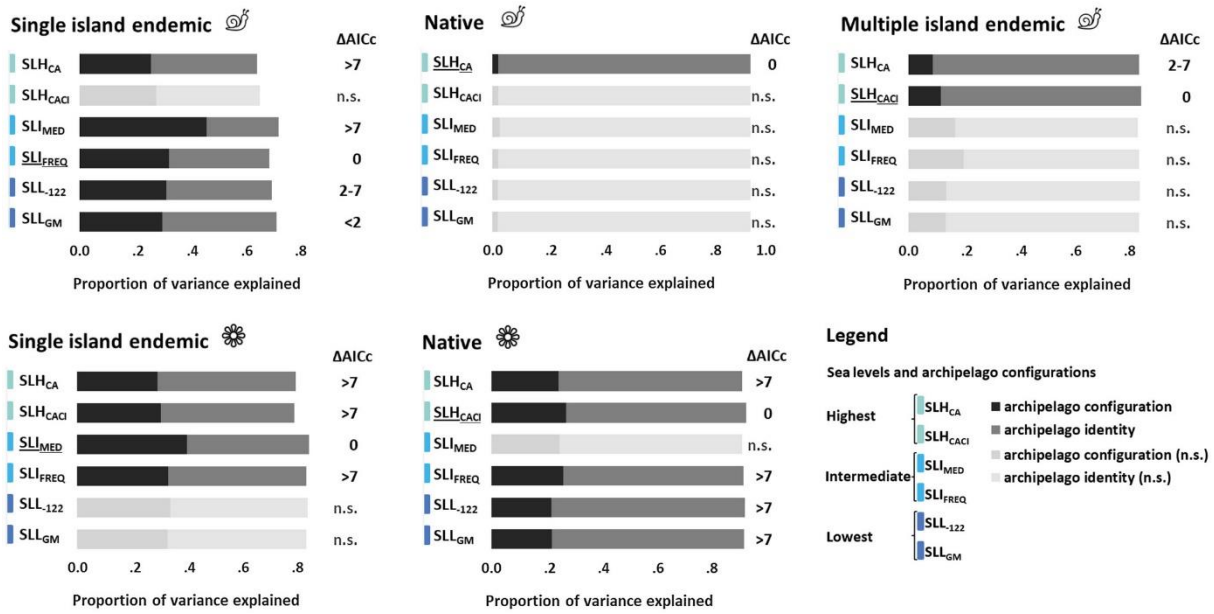

Figure 4. Performance of different archipelago configuration models for 53 islands in 12 archipelagos for land snails and angiosperms. To explain species richness in both taxa, we considered archipelago configuration models at the following sea levels: lowest [palaeo-configuration at −122 m mean sea level (MSL), SLL_{-122}; and at −134 m MSL, SLL_{GM}], intermediate (palaeo-configuration at the most frequent sea level, SLI_{FREQ}; and at the median sea level, SLI_{MED}) and highest (current area at present-day sea level, SLH_{CA}; and current area and isolation at present-day sea level, SLH_{CACI}). The size of each bar indicates the explained variance by archipelago configuration (R^2_M, darker shades) and archipelago identity ($R^2_C - R^2_M$, lighter shades). The difference in Akaike's information criterion corrected for sample size (Δ AICc) is provided for those models for which all predictors are significant ($p < 0.05$), or marked "n.s." for models for which not all predictors are significant (the bars of these non-significant models are greyed out).

The largest part of the variance in SIE richness for both taxa could be explained by palaeo-configuration at intermediate sea levels, supporting H2 (intermediate configuration and SIE). Although for SIE_S, the model SLI_{FREQ} had the lowest AICc, the largest part of the variance (73%) was explained by SLI_{MED}. Despite this model being outside Δ AICc < 7, it is the only model in which the variance explained by palaeo-configuration was larger than that explained by archipelago identity (47% and 26%, respectively; Figure 4). Also for SIE_P, the model SLI_{MED} explained the largest part of the variance (86%, of which 41% was explained by archipelago configuration and 45% by archipelago identity; Figure 4). In addition, this model also had the lowest AICc. As expected, palaeo-configurations at intermediate sea levels were able to explain a larger part of the variance than extreme configurations of a short duration. The performance of models for palaeo-configuration at lowest sea levels was generally poorer. For SIE_S, the variance explained by palaeo-configuration at lowest sea levels (32% for SLL_{-122}, 30% SLL_{GM}) was similar to SLI_{FREQ} (33%) but lower than SLI_{MED} (47%); the palaeo-configuration models at lowest sea level were within Δ AICc < 7 (Figure 4). Just as for SIE_S,

the variance in SIE_P explained by palaeo-configuration at lowest sea level (34% for SLL_{-122}, 33% SLL_{GM}) was similar to SLI_{FREQ} (34%), but lower than SLI_{MED} (41%). However, for SIE_P, none of the models for palaeo-configuration at lowest sea level was entirely significant.

The directionality of the relationships between the predictors in palaeo-configuration models (current area, CA; delta area, dA; palaeo-connectedness, PC) is consistent across taxa (Figure 5): richness of SIE_S and SIE_P increase with CA and dA, but decrease with PC. However, the effect size of CA and dA show opposing patterns for SIE angiosperms and land snails: CA has a larger effect on SIE_P, while dA has a larger effect on SIE_S (Figure 5). This is partly in line with our expectation that land snails would be more affected by palaeo-configurations than angiosperms ("H3: palaeo-configuration per taxon"). The contrast in effect sizes of CA and dA was consistent for other palaeo-configurations (Supporting Information Table S7).

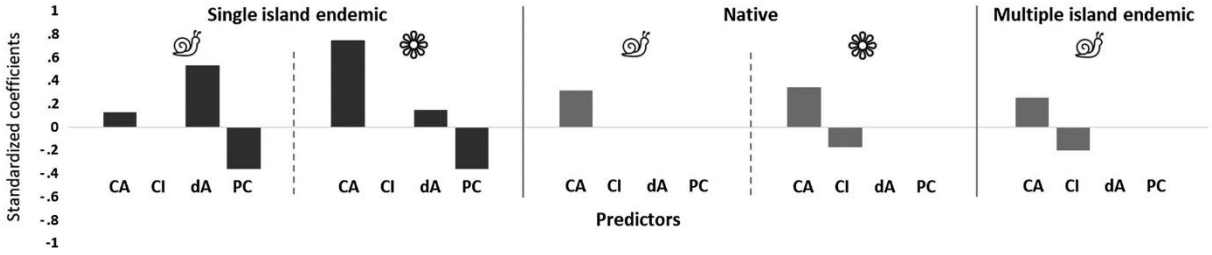

Figure 5. Bars indicate effect size of parameters in the best archipelago configuration models for 53 islands in 12 archipelagos for land snails and angiosperms. Standardized effect size of significant parameters ($p < 0.05$) in the model with lowest difference in corrected Akaike's information criterion (Δ AICc). The colours of the bars represent archipelago configurations at intermediate (dark grey) and highest (light grey) sea levels. Each model contains a selection of the following predictors: current area (CA), delta area (dA), palaeo-connectedness (PC) and current isolation (CI).

DISCUSSION

Our results are consistent with the hypothesis that palaeo-configurations at intermediate sea levels –which are representative of the Pleistocene—have left a stronger imprint on SIE_S and SIE_P richness patterns on volcanic oceanic islands than extreme archipelago configurations. This suggests that the relatively short-lasting configurations that have prevailed during the LGM are not sufficient to explain endemism patterns on volcanic oceanic islands.

Palaeo-configuration at different spatial scales of endemism

Our results conform to our first hypothesis that the signal of palaeo-configuration is stronger for SIE than for MIE and N. The proportion of the variance that could be explained by palaeo-configuration (R^2_M at intermediate and lowest sea level) was indeed larger for SIE than it was

for MIE and N. Ranking significant models based on AICc shows that for SIE, both models with palaeo-configuration and current configuration are within the set of most parsimonious models. In contrast, for MIE_S, N_S and N_P the set of most parsimonious models only contains configurations at present-day (highest) sea level. However, for these more widespread chorotypes, the variance explained by archipelago configuration was generally low (especially for N_S and MIE_S). For all archipelago configuration models across chorotypes (except SLI_{MED} for SIE_S), the largest part of the variation is explained by the identity of the archipelago (random effects in the model), suggesting that other factors besides archipelago configuration (e.g., climate, geological dynamics, distance from the mainland, island age, human impact, etc.) probably play an important role in shaping current diversity patterns on oceanic islands. These findings suggest that archipelago configuration is an important factor related to patterns of single-island endemics but less so for (non-endemic) natives. Furthermore, for SIE, those palaeo-configurations that are representative of the Pleistocene are more relevant than short-lasting configurations (Figure 6).

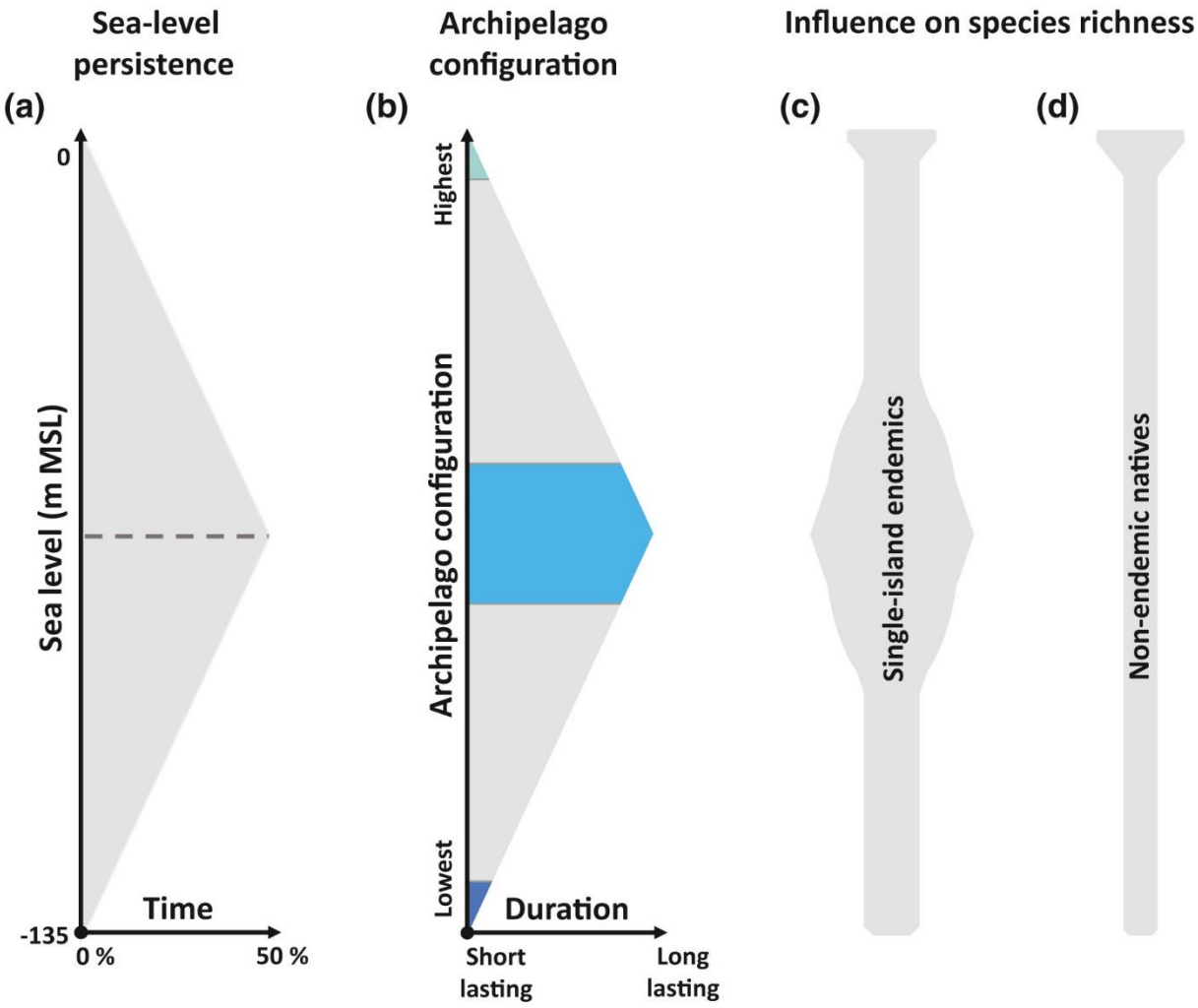

Figure 6. Conceptual figure illustrating the influence of sea-level driven changes in archipelago configuration on species richness patterns of single-island endemics and non-endemic natives. (a) The percentage of time the sea level was either above or below a certain level. (b) The duration of an archipelago configuration as shaped by sea-level fluctuations. (c, d) The width of the bars indicates the importance of an archipelago configuration (b) in shaping single-island endemic and non-endemic native richness.

Persistence and recurrence of palaeo-configurations

Palaeo-configuration at lowest (glacial maxima) sea level had a weaker explanatory power on SIES than intermediate configurations (noting the small Δ AICc between models for SIE_S), and a weak non-significant effect on SIE_P. This supports our second hypothesis that palaeo-configurations that are more representative of the Pleistocene, associated with intermediate sea levels, have left a stronger signal than extreme configurations of a short duration. Our findings contrast with those of Weigelt et al. (2016), who reported that the number of SIE_P could be explained by palaeo-configuration at a sea level of −122 m below today. The difference might be explained by the fact that we selected a subset of angiosperm data

exclusively from volcanic oceanic islands, thus preventing confounding geological or genetic effects derived from mixing with islands of other geological origins (Ali, 2017; Whittaker & Fernández-Palacios, 2007). On continental fragments in particular, differences in bathymetry lead to dissimilar responses to cyclic sea-level fluctuations. The granitic Seychelles are a case in point illustrating the drastic area change and PC of continental fragments (Warren et al., 2010). However, the most important reason for the poor performance of models based on palaeo-configuration at lowest sea levels compared to intermediate configurations is probably related to the short lasting and interruptive character of glacial maxima.

Intermediate palaeo-configurations were reconstructed at the SLI_{MED} and the SLI_{FREQ}. Palaeo-configuration at SLI_{MED} explained most of the variance (R^2_M) for both SIE_S and SIE_P. Also in terms of AICc intermediate palaeo-configurations performed best for SIE; however, for SIE_S, SLI_{FREQ} had the lowest AICc, while for SIE_P, SLI_{MED} had the lowest AICc. Although both R^2_M and AICc suggest that it is worthwhile to consider palaeo-configurations at intermediate sea levels for understanding present-day patterns of SIE richness, they do not provide conclusive evidence regarding the best choice of approach. We anticipate that future studies focussed on specific archipelagos (and other taxa) will shed more light on which sea levels are most relevant in a particular archipelagic context. We hypothesize that the answer will depend on the sea-level thresholds at which island area and connectedness change significantly.

Contrasting roles of palaeo-area and palaeo-connectedness across taxa

Sea-level fluctuations in the past have modified island area and isolation simultaneously. However, when considering these elements of archipelago configuration separately, it becomes clear that SIE richness of both land snails and angiosperms increases with CA and dA, but decreases with PC. Although CA and dA both hold a positive relationship with SIE_S and SIE_P richness, dA has a larger statistical effect on SIE_S, while CA is most important for SIEP (cf. Kreft, Jetz, Mutke, Kier, & Barthlott, 2008). This finding is consistent with our third hypothesis that land snails will be more affected by palaeo-configuration than angiosperms. As already mentioned in the Introduction, this pattern may be explicable in relation to general differences in speciation and dispersal between the two taxa; land snails tend to be able to speciate at smaller spatial scales than most angiosperms (Kisel & Barraclough, 2010). Hence land snails can produce more SIE in any given island area, and show stronger effects of island area being formerly larger than do angiosperms. Conversely, a greater mobility of plants

could connect "would-be endemics" or replace them with fresh colonists and as such reduce the effect of area change. This reasoning seems in line with the chorotype proportions for SIE in our dataset, which are high for land snails and low for angiosperms. An interesting avenue for future research would be therefore to further explore the underlying mechanisms that might explain the differential response of both taxa to palaeo-area. Our results indicate a negative relationship between PC and SIE richness of both taxa. The decreasing number of SIE_S and SIE_P with PC might result from higher levels of gene flow, hindering diversification into distinct lineages (cf. Heaney et al., 2005). This agrees with a recent study on the Puerto Rico Bank where repeated connectedness and fragmentation impeded divergence and speciation of ground crickets (Papadopoulou & Knowles, 2017). Alternatively, elevated biotic interchange following climatic fluctuations and geographical rearrangements over the Pleistocene might have resulted in local extinctions (Vermeij, 1991). Weigelt et al. (2016) also found a negative relationship between palaeo-connectedness and SIE_P and concluded that this result falsifies the species pump hypothesis, that is, that repeated separation and connectedness drive speciation (Gillespie & Roderick, 2014; Qian & Ricklefs, 2000). However, it may also be explained by the fragmentation of a population of a SIE species on a palaeo-island into subpopulations, changing the chorotype from SIE to MIE as sea levels rose towards the current interglacial high sea level (Figure 2).

Archipelago configuration models containing PC as a predictor performed better for SIE than those containing current isolation. This suggests that the actual fusion and splitting of islands may be more important as a moderating factor reducing numbers of SIE than the proximity of islands within an archipelago. Our findings correspond to Heaney et al. (2005) who found little genetic variation among mammal populations on Philippine islands that were merged during lower sea levels, while populations on islands that were never connected (but sometimes in close vicinity) showed more genetic differentiation. A similar conclusion was reached by Rijsdijk et al. (2014) who found that the proportion of MIE/SIE plants shared between Fuerteventura and Lanzarote (which were joined in the palaeo-island Mahan) is significantly larger than all other Canary island pairs that were never connected.

Island- and archipelago-specific factors

Glacial–interglacial cycles over the Pleistocene have simultaneously influenced the geography of all islands globally. However, there are many regional factors shaping differences in

insular biodiversity patterns among and within archipelagos. Islands commonly occur in archipelagos that exhibit biogeographical coherence, that is, similar patterns, in species diversity as a result of shared climate, distance from the potential species pool, intra-archipelagic isolation and geological history (Ali, 2017; Heaney et al., 2013; Triantis et al., 2015). In our analyses archipelago identity explained a large part of the variance (random effect in linear mixed models), highlighting the importance of accounting for among-archipelago variation (Bunnefeld & Phillimore, 2012; Cameron et al., 2013).

Regarding the within-archipelago differences, geological dynamics arguably have a large role in shaping island geography and archipelago configuration. For example, geological processes of plate tectonics, volcanism, subsidence and erosion may drive major changes in island geography and archipelago configuration (Borregaard et al., 2017; Carracedo, 2014; Gillespie & Clague, 2009; Gillespie & Roderick, 2002; Price, Clague, Bay, Road, & Landing, 2002; Stuessy, 2007; Whittaker et al., 2008, 2017). While general developmental trends may be identified for particular classes of oceanic islands (Whittaker et al., 2008, 2017), in practice, island ontogeny and volcanic activity are island specific. For example, the eight main islands of the Hawaiian archipelago show linear age progression from east to west and range in age between 0.5 Ma (Hawaii Island) and 5.1 Ma (Kauai). Hawaii itself is the only island that is volcanically active, all others being disconnected from the hotspot and inactive for at least 0.75 Myr. This contrasts with the complex geological setting of the Azores, with a western group of two islands located on the North American plate, and a central and eastern group (of five and two islands, respectively) located at the junction between the Eurasian and Nubian lithospheric plate (Ramalho et al., 2017), and no linear age progression from one side of the archipelago to the other (Ávila et al., 2016). In addition, some islands in our dataset are younger than the last nine glacial–interglacial cycles (~800 ka) we used to calculate the most frequent and median sea levels. However, due to the recurrent character of sea-level oscillations, later stages of these cycles will nonetheless have affected younger islands. Incorporating glacial–interglacial driven changes in island geography becomes challenging as longer time-scales are considered because they overlap and interact with geological dynamics. For future studies it will be important to include greater detail on regional geological dynamics that have shaped archipelago configuration in the past.

CONCLUSION

To our knowledge this is the first time that the effects of long- and short-lasting archipelago configurations on species richness patterns have been compared at a global scale across multiple archipelagos. Although we included in our study 53 volcanic oceanic islands with different geological histories, we still found a consistent pattern for the two taxa considered: palaeo-configurations at intermediate sea levels have left a stronger imprint on single-island endemic richness patterns than extreme archipelago configurations of short duration, whereas non-endemic (native) species richness was generally poorly explained by palaeo-configuration. These findings support intermediate palaeo-configurations as most relevant for understanding present-day patterns of endemic biodiversity across volcanic oceanic islands. Further research is required to explore how these environmental dynamics may have influenced other archipelagos and taxa. Previous studies have acknowledged that islands were larger and less isolated in the past, but have generally overlooked the potential significance of the duration of different palaeo-configurations. Our results suggest that for understanding evolutionary dynamics of insular biota it is relevant to look beyond extreme palaeo-configurations that persisted for only a few thousand years (such as the LGM) and to test for biological legacies of alternative palaeo-configurations.

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PART 2

ISLAND BIOGEOGRAPHY IN THE ANTHROPOCENE

INTRODUCTION TO PART 2 OF THIS THESIS

After the term 'Anthropocene' was coined at the turn to the 21st century (Crutzen & Stoermer, 2000; Crutzen, 2002), the concept has been adopted by scholars from the social sciences, natural sciences and humanities. Today, 'the Anthropocene' appears widely in popular media as a catch-all phrase to denote the changing relationship between people and the rest of nature (Malhi, 2017). Although the Anthropocene has the potential to bring together people from different knowledge domains, in practice it has also caused confusion and fierce debate (Malhi, 2017). There are many nuances to this debate, but broadly speaking, the contrasting perspectives can be divided in two groups. The first perspective is mainly concerned with global environmental changes in the Earth system (Steffen *et al.*, 2007; Zalasiewicz *et al.*, 2011). Viewed from this perspective, the Anthropocene means something very specific: a stratigraphic unit in the Geologic Time Scale (Figure 1).

Cenozoic Era (65 Ma)	**Quaternary Period (2.58 Ma)**	**Anthropocene (?)**	**1950: Great acceleration, extensive nuclear tests** (Zalasiewicz *et al.*, 2015) **1800: Industrial revolution** (Steffen *et al.*, 2007) **1492: First contact between Old- and New World** (Lewis & Maslin, 2015; Moore, 2015, 2017)
		Holocene Epoch (0.01165 Ma)	**~10.000 BP onwards: Plant and animal domestication, spread of agriculture** (Smith & Zeder, 2013; Stephens *et al.*, 2019)
		Pleistocene Epoch (2.58 Ma)	**~50.000BP onwards: Megafauna extinctions** (Dirzo *et al.*, 2014; Malhi *et al.*, 2016; Araujo *et al.*, 2017)

Figure 1. Most recent time units of the Geologic Time Scale (Walker et al., 2018) with some key global socio-environmental transitions added. Note that the length of the segments in the figure do not represent the duration of the different time units. Others have produced visualizations of the Geologic Time Scale and added the proposed Anthropocene (Lewis & Maslin, 2015), or provided a timeline with proposed starting dates for the Anthropocene (Smith & Zeder, 2013; Braje, 2015; Malhi, 2017). Here I have combined them into one graphic. Rather than using the term 'starting dates' I prefer 'global socio-environmental transitions' to underline that

each of these events marks a change in the relationship between people and the environment (regardless of the eventual marker for the start of the Anthropocene).

The Geologic Time Scale is used to divide Earth's history of 4.6 billion years into distinct time intervals: eons, eras, periods, and epochs. If the Anthropocene would become a formal stratigraphic unit, it would become the most recent epoch of the Quaternary Period, and would put an end to the Holocene – the epoch we are now formally living in (alternatively, the Holocene could become a stage of the Pleistocene Epoch, see: Lewis & Maslin, 2015). For the Anthropocene to be included in the Geologic Time Scale, its onset has to be defined, and subsequently ratified by the International Commission on Stratigraphy (Zalasiewicz *et al.*, 2008). While the onset of the Anthropocene is still much debated, the Anthropocene Working Group seems to favours a mid-twentieth century (Zalasiewicz *et al.*, 2015). In contrast, a second perspective emphasizes the underlying societal causes of global changes at local and regional scales (Smith & Zeder, 2013). Scholars from this perspective criticise the approach to ratifying the Anthropocene because it would mask the deep historical roots of human-environment relationships (Figure 1), and the large variability between people and regions (Malm & Hornborg, 2014; Braje, 2015; Ellis *et al.*, 2016). A possible approach to reconcile these two contrasting perspectives, might be to explore how local and regional human-environment interactions have accumulated to shape global changes, and how global changes manifest at finer spatial scales. In this second part of the thesis, I will use islands as model systems to study the biodiversity outcomes of local human-environment interactions. Therefore, the research question I address in this part is as follows:

How have human-environment interactions shaped island ecosystems and landscapes?

Two characteristics shared by islands worldwide make them ideal model systems for answering questions about human-environment interactions in the context of global change. First, islands are among the last places on Earth to be settled by humans, and therefore the history of human-environment interactions is condensed in a few centuries to millennia. This allows for a reconstruction of past human influence on biodiversity and for comparing them to pre-human baselines (Nogué *et al.*, 2017). Secondly, islands can be viewed as natural experiments (Diamond, 1983; Diamond & Robinson, 2010; Kueffer *et al.*, 2013), because around the world there exist thousands of replicates that differ regarding their societal and environmental conditions. This spatial heterogeneity allows for comparing ecological outcomes of human-environment interactions across multiple islands (Kueffer & Fernández-Palacios, 2010). The two studies presented in the following sections benefitted from either

one of the previously mentioned island characteristics (short-lasting human history, environmental and societal variability among islands).

The first study is a historical analysis of human-environment interactions on Mauritius, Indian Ocean (section 2.2; Norder *et al.*, 2017). This single-island case-study is followed by a comparative analysis of 30 islands in the Atlantic Ocean (section 2.3; Norder *et al.* in revision). These islands are particularly interesting in the context of global change because they were important as replenishment stations following the 15th century while global maritime trade relied on sailing vessels. Mauritius, for example, was an important entrepôt, and formed the gateway towards the Indian Ocean (Grove, 1996), while the Atlantic Ocean Islands were crucial hubs in connecting the Old- and New World (Crosby, 1972, 1984). For Mauritius, the environmental and societal developments following the settlement of the island in the early 17th century are relatively well-documented. I use data on historical deforestation to model the cumulative soil loss resulting from land cover change, and compare it to the amount of soil loss under pre-human conditions (section 2.2; Norder *et al.*, 2017). Cumulative soil loss is a suitable proxy for ecosystem status because it affects the functioning of terrestrial and marine ecosystems and the services they provide to society (Millennium Ecosystem Assessment, 2005; Montgomery, 2007, 2012; Braimoh & Vlek, 2008). As such, my analysis of Mauritius will provide insight in the historical evolution of human-environment interactions and their ecosystem consequences. Previous studies aimed at understanding human impact on ecosystems have emphasized the role of societal drivers, while often neglecting the potential role of environmental variables (but see: Rolett & Diamond, 2004). Therefore, in section 2.3 (Norder *et al.* in revision) I will assess the relative contribution of environmental and societal factors in shaping the extent of native ecosystems across islands.

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2.1 Assessing temporal couplings in social–ecological island systems: historical deforestation and soil loss on Mauritius (Indian Ocean)

Norder S.J., Seijmonsbergen A.C., Rughooputh, S.D.D.V., van Loon E.E., Tatayah, V., Kamminga, A.T., Rijsdijk K.F. (2017). Assessing temporal couplings in social-ecological island systems: historical land use change and soil loss analyses on Mauritius (Indian Ocean). Ecology and Society 22, 29-45. https://doi.org/10.5751/ES-09073-220129

SJN designed the study, analysed the data and interpreted the results. SJN wrote the manuscript with input from all co-authors.

ABSTRACT

Temporal couplings, such as historical interactions between deforestation and soil loss, are responsible for the current state of a wide range of ecosystem services of the social–ecological system on Mauritius. Islands are suitable study sites for understanding temporal couplings and telecouplings because of their: (1) clearly defined physical boundaries, (2) finite local resources, and (3) relatively short human history. Six well-documented historical deforestation maps, starting from the first colonization of Mauritius in 1638, were used as input parameters to model two scenarios of cumulative soil loss, with and without deforestation, using the revised universal soil loss equation in a geographic information system. The scenarios show that historical deforestation since 1638 has resulted in a cumulative soil loss that drastically exceeds soil loss under a natural baseline scenario without deforestation. The adopted method illustrates to what extent the current state of the soil of a social–ecological system is negatively affected by past human–environment interactions. We suggest that potential negative impacts on insular societies are mitigated by telecouplings such as food, fuel, and fertilizer imports.

Key words: deforestation; historical soil loss; islands; Mauritius; RUSLE; social–ecological systems; telecouplings; temporal couplings

INTRODUCTION

Soils provide ecosystem services, such as water and nutrient retention, and form a substrate for agriculture (Millennium Ecosystem Assessment 2005, Braimoh and Vlek 2008). Soil loss, therefore, undermines the provisioning of many ecosystem services on which human well-being depends. Examples are negative impacts on agricultural productivity and soil quality by a reduction in nutrients, organic matter, soil biota, soil depth, infiltration rates, and water-holding capacity (Pimentel et al. 1995). Soil loss not only affects terrestrial ecosystem services, but marine ecosystem services as well. Increased sediment influx in the coastal zone leads to unwanted and increased turbidity and nutrient concentrations (Ramessur 2002, Fabricius 2005, Nagelkerken 2006, Liu et al. 2007b, Erftemeijer et al. 2012). Although natural soil loss is balanced by the process of soil formation, soils can be considered a limited natural resource because soil formation is a slow process (Montarella 2015). In general, rates of soil formation are closely correlated with erosion rates under native vegetation and the pace of erosion over geologic time, whereas erosion rates under agricultural practices are much higher (Montgomery 2007). Quantification of soil loss under native forest, therefore, provides a baseline to which human-induced soil loss can be compared.

Quantification of the responses of a social–ecological system (SES) to land-use change and deforestation is important for making informed decisions about balancing human demands and ecosystem functioning (DeFries et al. 2004). It is widely acknowledged that the current state of a SES is the outcome of patterns, processes, and decisions in the past (Foster et al. 2003, Kirch 2007, Rounsevell et al. 2012, Steen-Adams et al. 2015). The cumulative and evolving impacts of historical interactions within a SES on present and future conditions are termed legacy effects (Liu et al. 2007a), which suggests that the present-day soil is partly degraded as a result of deforestation and agricultural practices in the past. However, the impact of soil degradation may remain unnoticed because of time lags between historical social–ecological couplings and their current effects (Liu et al. 2007b, Raudsepp-Hearne et al. 2010, Steen-Adams et al. 2015). These legacy effects and time lags are two important aspects for understanding temporal couplings in a SES (Liu et al. 2007a, Steen-Adams et al. 2015).

The current state of an island SES is also shaped by telecouplings; socioeconomic and environmental interactions with other SES over spatial distances (Liu et al. 2013, Eakin et al. 2014, Friis et al. 2016). These telecouplings, such as increased global economic connectivity, complicate the interplay between drivers and consequences of land-system change (Lambin

and Meyfroidt 2011, Meyfroidt et al. 2013). Taking telecouplings into account helps to acknowledge that ecosystem services can be partly substituted in space by food and fuel imports and enables a decoupling of a society from its local ecosystem. As a result, time lags between soil degradation and its perceived societal impact may increase. It can, therefore, be hypothesized that the continued reliance on telecouplings allows for the development of a 'soil debt', which is a net decrease of the total soil stock in a region over time, that results when erosional rates exceed soil formation rates. The debt can be paid when conditions promoting soil recovery, such as reforestation, are restored.

Islands provide ideal conditions for understanding the complex historical couplings between humans and their natural environment because of three island characteristics (Kirch 1997, Fitzpatrick and Keegan 2007, Royle 2012, Warren et al. 2015): (1) clearly defined physical boundaries; (2) finite local resources, such as land, soil, water, and timber; and (3) for many islands, a relatively recent human colonization history. Many island ecosystems have been drastically transformed following human colonization (Strasberg et al. 2005, Caujapé-Castells et al. 2010). Additionally, human colonization can coincide with a substantial increase in erosion and sedimentation (Lepofsky et al. 1996, Kahn et al. 2015), resulting in drastic alteration of the landscape and ecosystem functioning. On Mauritius, human settlement is closely linked to forest fragmentation, fires, introduction of exotic species, and degradation of natural ecosystems (Cheke and Hume 2008, Rijsdijk et al. 2011, 2015, Florens et al. 2012, De Boer et al. 2013). These human impacts eventually affect the ecosystem's capacity to provide services to society. The introduction of exotic species, for example, has been shown to negatively influence supporting, provisioning, cultural, and regulating services (Vilà et al. 2010). The objective of this paper is to analyze the effects of temporal couplings on the current state of an island SES. In addition, we will assess how far the capacity of the soil to provide ecosystem services to Mauritian society is undermined. Mauritius forms an ideal study site for such an analysis because its social–economic and deforestation history are relatively well documented. This allowed for an historical analysis of human–environment interactions and the role of telecouplings. Temporal couplings on Mauritius were operationalized by quantifying the influence of historical deforestation on cumulative soil loss. Comparison of the cumulative soil loss resulting from deforestation to natural background variation yields insight into the degree of human impact on island ecosystems and environments (Swetnam et al. 1999, Connor et al. 2012). The history of human–environment interactions on Mauritius, including the role of telecouplings, is included in this comparison.

Historical human–environment interactions and telecouplings

The island Mauritius (1865 km2) is located in the Indian Ocean approximately 860 km east of Madagascar and measures roughly 50 by 60 km (Figure 1). The climate on Mauritius has two seasons: a rainy summer (70% of annual rainfall) from November to April dominated by cyclone passage, and a dry winter from May to October (Nigel and Rughooputh 2010). The central plateau and the eastern part of the island receive the highest annual precipitation (Figure 1).

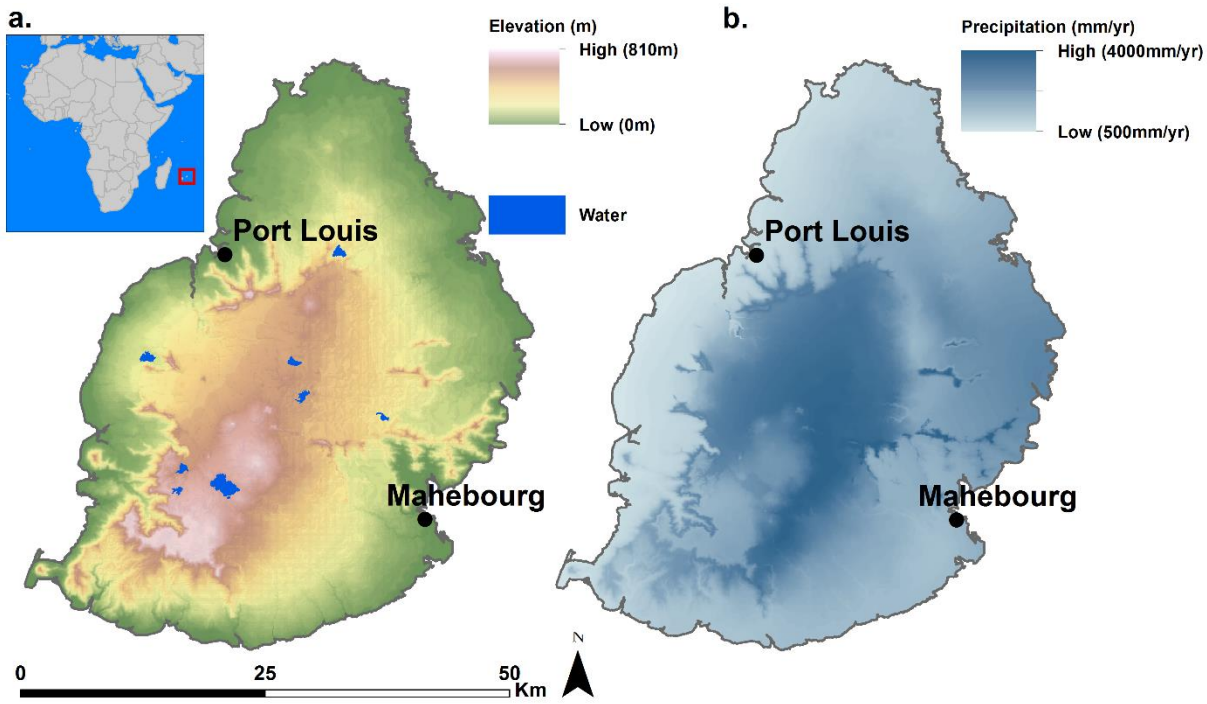

Figure 1. Elevation map of Mauritius (left panel) and annual precipitation averaged over 30 years (right panel). Left panel is based on data from Seul (1999) and Hill (2001), right panel is based on data from Padya (1984) and Mauritius Meteorological Services (2005).

Mauritius was first colonized in 1638 by the Dutch, who used the island mainly as a refreshment station. A variety of crops were introduced, such as tobacco, sweet potato, and sugar cane (Brouard 1963). Domestic animals and deer were brought to the island, the giant tortoises that grazed the coastal areas were killed for their meat, and trees in the lowland coastal forests were felled to be exported. The first felling of trees occurred in the direct surroundings of the harbors near present-day Mahebourg (Grand Port District) and Port Louis (see deforestation maps in Figure 2, lower panel). Although deforestation occurred at a slow pace and was localized (Griffiths and Florens 2006), nearly all accessible large black ebony (Diospyros tessellaria) trees were felled (Brouard 1963, Moree 1998). In this period, only a

few hundred colonists permanently inhabited Mauritius under Dutch rule (Figure 2, upper panel), and eventually, the island was abandoned in 1710.

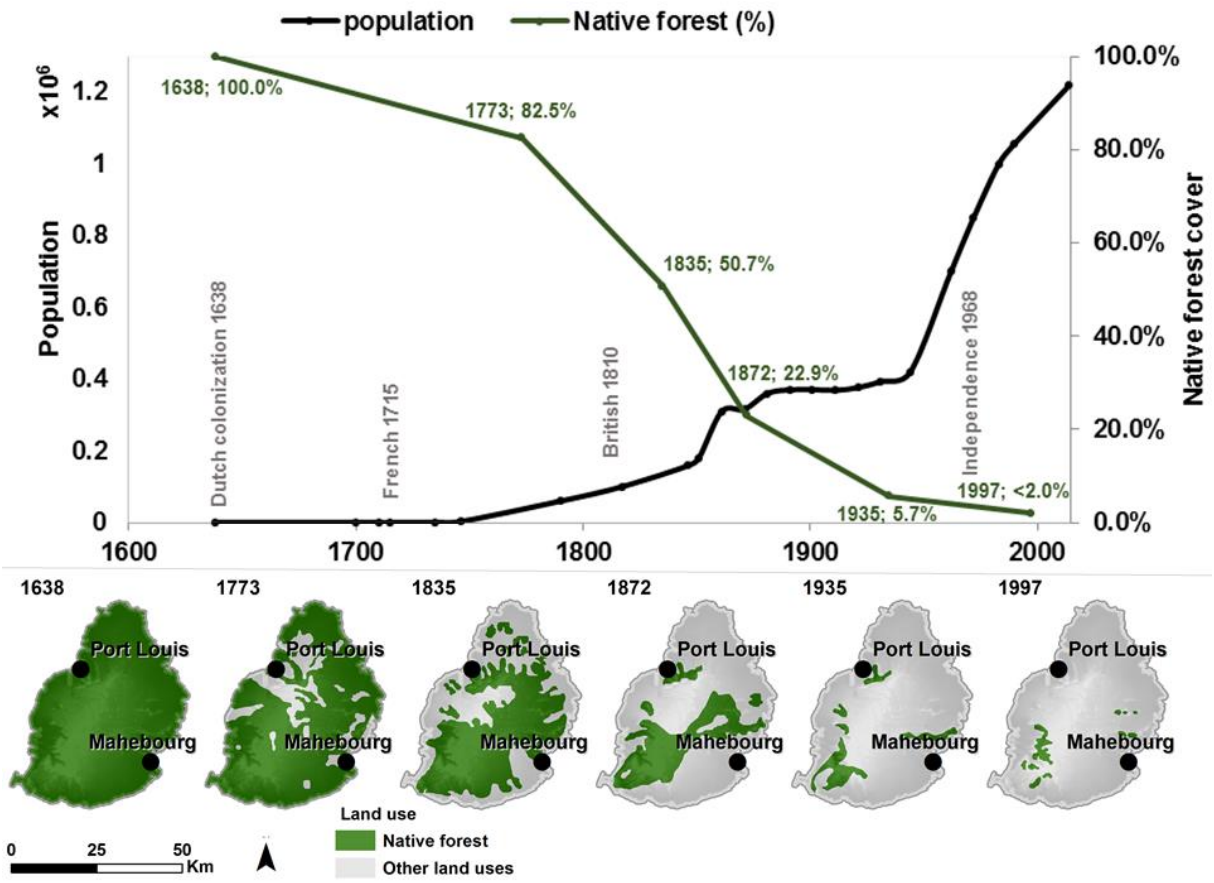

Figure 2. Population growth and deforestation on Mauritius since human colonization (upper panel). Population graph based on Koenig (1944), Titmuss and Abel-Smith (1960), Lutz and Wils (1994), and Statistics Mauritius (2015a), percentage of native forest cover from Florens (2013). The lower panel shows six timeslices indicating the areas where native forest was removed since colonization in 1638. The six maps are based on Vaughan and Wiehe (1937) and references therein, and Page and D'Argent (1997).

After Mauritius was abandoned by the Dutch, it was claimed by France in 1715 and settled in 1721. Mauritius functioned as a trading post to supply French ships in the Indian Ocean with essential goods and services (Allen 1989). Mauritius's role as a commercial entrepôt greatly promoted local economic activity and laid the foundation for the formation of domestic capital (Allen 2008). Local merchants and seafarers made investments in agricultural land (Allen 2008), and some public land concessions were given out freely to settlers (Grove 1996). The local economy was primarily occupied with providing goods and services to the ships that made a stopover in the harbors, and the local government actively encouraged the cultivation of sugar, spices, and other crops (Allen 1989, 2008). Sugar cane became the preferred and dominant agricultural crop, and a plantation system was introduced. The French

brought slaves from Madagascar, Mozambique, and West Africa to Mauritius primarily to work on the sugar cane plantations (Addison and Hazareesingh 1993). Deforestation continued, not only to make room for sugar cane plantations, but also to meet the growing timber demand for naval and construction purposes (Grove 1996).

The French plantation system became more institutionalized after Mauritius was conquered by the British in 1810 (Alladin 1986). This marks the beginning of a transformation from a trade-oriented economy toward a plantation economy, predominantly focused on sugar production for the British imperial market (Allen 2008). Slaves continued to form the primary workforce on the sugar cane plantations. By 1817, 80,000 slaves lived on Mauritius, out of a total population of nearly 100,000 (Lutz and Wils 1994, Teelock 1998). Major expansion of sugar cane occurred after 1825 when the British government allowed the import of Mauritius sugar and removed the tax penalty in Britain (Allen 1989). In addition, sugar consumption started to increase profoundly in Britain, which transformed sugar cane into a main cash crop (Addison and Hazareesingh 1993). Sugar exports became the predominant contributor to the Mauritian economy. After 1830, sugar contributed 85–90% to export earnings (Allen 2008); from that moment onward, almost all food and other consumer products were imported (Brookfield 1959). As a result of the intensification of sugar cane agricultural activities in the 19th century, deforestation increased drastically (Florens 2013). The agricultural regions expanded mainly in the accessible coastal areas, leaving the central areas covered with forest (Brookfield 1959). Starting in 1834, after the abolition of slave labor, the British brought indentured laborers from India to form the primary workforce on the plantations. From the 1870s onward, large sugar estates started selling their less productive land to smallholders, driven by labor shortages and a decreasing sugar price due to competition with European sugar beet (Addison and Hazareesingh 1993, Meisenhelder 1997). This period, referred to as the "Grand Morcellement," led to the establishment of a large number of smallholder farms. By the early 1920s, almost half of the area under sugar cane was cultivated by smallholders of Indian origin (Brookfield 1959, Allen 2008). However, the land division was highly unequal; in 1946, there were 30 factory estates, 109 large estate planters, and 13,685 planters owning small plots of often marginal quality (Brookfield 1959).

In 1968, the year of independence, sugar accounted for 93% of the nation's exports (Meisenhelder 1997), whereas in 2014 this was only 3.85% (Mauritius Chamber of Commerce and Industry 2015). Whereas the area under sugar cane remained relatively stable around 80,000 ha (43% of land area) between the year of independence and 1980, this area

decreased rapidly in the last decades from 76,840 ha (41.5%) in 1990 to 50,687 ha (27.4%) in 2014 (Statistics Mauritius 2012, 2013a, 2014). During the 1970s and 1980s, the Mauritian economy underwent major structural changes, with a rapid phase of industrialization, diversifying into two major activities, textiles and tourism (Ramessur 2002). With the diversification of the economy, vegetated areas on Mauritius have been converted to other land uses, mainly for urban developments like roads, hotels, and housing (Hammond et al. 2015). These economic changes were accompanied by rapid population growth (Fig. 2, upper panel). Today, the population of Mauritius has risen to 1,219,659 people (Statistics Mauritius 2015a). On top of this, tourist arrivals have doubled in the last two decades, from 486,867 in 1996 to 1,038,968 in 2014 (Statistics Mauritius 2013b, 2015b). Much of the food that is needed to feed the growing population is being imported. Both in volume and monetary terms, import of most foodstuffs such as cereals, fruits, nuts, vegetables, dairy, and meat products largely exceeds exports (Mauritius Chamber of Commerce and Industry 2015).

METHODOLOGY

To model historical soil loss scenarios, we adopted the widely applied revised universal soil loss equation (RUSLE; Renard et al. 1997). We use the RUSLE because it has successfully been applied in soil erosion studies on Mauritius before (Le Roux et al. 2005, Nigel and Rughooputh 2012). By using six historical deforestation maps, 12 monthly precipitation maps, a digital elevation model (DEM), and a soil map as input parameters for the RUSLE, two cumulative soil loss scenarios were constructed (Figure 3).

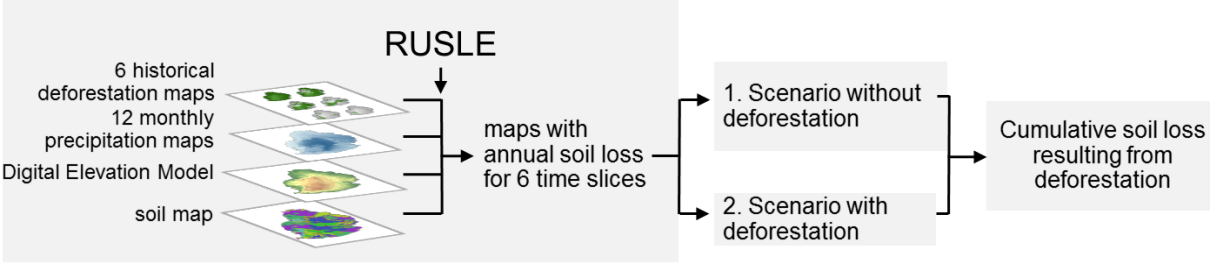

Figure 3. Workflow illustrating the RUSLE-based analysis of cumulative soil loss for two scenarios of deforestation on Mauritius.

The first scenario ("scenario without deforestation") represents a situation in which Mauritius would never have been colonized and the entire island remained covered with native forest. The soil loss in 1638 was used as the annual soil loss rate to calculate the cumulative soil loss for the scenario without deforestation. The second scenario, with deforestation, represents a situation in which forest is gradually converted to sugar cane. For this scenario, six historical

deforestation maps showing native forest from the years 1638, 1773, 1835, 1872, 1935, and 1997 (Vaughan and Wiehe 1937, Page and D'Argent 1997) were digitized and georeferenced to construct input parameters for the RUSLE. The modeled soil loss for these timeslices was used as annual soil loss rates to reconstruct the cumulative soil loss for the scenario with deforestation. Linear interpolation was used to reconstruct soil loss rates for the intermediate years between the modeled timeslices. Comparison of both scenarios provides insight into the extent to which historical deforestation impacts cumulative soil loss because the timeframe and parameters for soil type, precipitation, steepness, etc. are the same in both scenarios. These cumulative soil loss scenarios provide a proxy of the legacy effects of historical deforestation.

We have automated the soil loss modeling workflow using the RUSLE in ArcGIS 10.1 model builder. The RUSLE (Renard et al. 1997) equals:

$$A = R \times K \times LS \times P \times C$$

where A is the computed soil loss (t ha-1 year-1), R is the rainfall erosivity factor (MJ mm ha-1 h-1 year-1), K is the soil erodibility factor (t ha MJ-1 ha-1 mm-1), LS is the topographic factor (unitless), P is the support practice factor (unitless), and C is the cover management factor (unitless). Soil loss has been calculated on a monthly basis and is subsequently aggregated per year. An overview of the data sources where the RUSLE input parameters are derived from is presented in Table 1. Here, the transformation steps carried out to prepare the input data for the RUSLE are briefly discussed; a more extensive overview of the methodology is presented in Table A1.1. (Appendix 1). The RUSLE model and input data are shared in the supplementary materials (Appendix 2).

Table 1. *Metadata and sources* used to develop input maps for the RUSLE. A detailed description of data transformations to develop RUSLE factors can be found in Table A1.1 in Appendix 1.

Factor	Data source
R	Precipitation data from Mauritius Meteorological Services (2005) and Padya (1984).
K	Digitized vector map with spatial distribution of soil types from Willaime (1984).
	Soil erodibility factors from Nigel and Rughooputh (2012).
LS	Digital Elevation Model (DEM) of Mauritius based on the work of Seul (1999) and Hill (2001).
P	Land-use distribution for six timeslices from Vaughan and Wiehe (1937) and references therein, and Page and D'Argent (1997).
	Support practice factor from Nigel and Rughooputh (2012).
C	Land-use distribution for six timeslices from Vaughan and Wiehe (1937) and references therein, and Page and DÙArgent (1997).
	Cover management factor from Nigel and Rughooputh (2012).

Rainfall is the driving factor for initiating sheet and rill erosion (Yang et al. 2003). R represents the kinetic energy of rainfall and was calculated by using a modified Fournier index (Arnoldus 1977, 1980). Precipitation data from Mauritius (Padya 1984, Mauritius Meteorological Services 2005) indicate that this index closely coincides with calculated R values for the climate stations Curepipe, Vacoas, and Plaisance on Mauritius (Atawoo and Heerasing 1997). K represents the soil loss specific to a soil type, measured on a standard plot. The soil map comes from Willaime (1984), erodibility factors have been extracted from Nigel and Rughooputh (2012). The LS factor combines slope length (L) and slope steepness (S). These factors are calculated from a 100 x 100 m resolution DEM, which is based on the work of Seul (1999) and Hill (2001). The geomorphological zonation of Saddul (2002) indicates that sedimentation is dominant on <3% slopes, which was accounted for in the model by deselecting slopes <3% from the soil loss classes. Another additional adaptation is that lakes were excluded from the flow length calculation using a Boolean operator and a digitized lake data set. The urban area of Port Louis has been masked as well. The values for P and C are representative for a particular land-use type and reflect local agricultural practice. Values for the support practice factor of two land-use types (sugar cane and native forest) on Mauritius are based on the work of Nigel and Rughooputh (2012). Subsequently, these P and C values have been assigned to the land-use types in historical deforestation maps (Fig. 2, lower panel) georeferenced and digitized from Vaughan and Wiehe (1937) and Page and D'Argent (1997). For further details and parameter specific equations of the RUSLE, we refer to Arnoldus (1977), Wischmeier and Smith (1978), and Renard et al. (1997).

Some generalizations were necessary to quantify the effects of historical deforestation on soil loss during a period of nearly four centuries. Even though historical deforestation on Mauritius is relatively well documented, most generalizations stem from the limited detail of

historical maps. First, while different forest types existed, no distinction is made. The native forest before human settlement consisted of dry palm woodlands on the leeward side of the island, inland semidry evergreen forest, and high-elevation wet forests (De Boer et al. 2013). Although Mauritius was almost entirely forested before human settlement (van der Plas et al. 2012), it is known that heath and marshy vegetation covered substantial areas (Vaughan and Wiehe 1937, De Boer et al. 2013). In addition, the coastal habitats were likely inhabited by a plant community of grasses and herbs grazed by the currently extinct giant tortoises Cylindraspis inepta and C. triserrata (Hansen et al. 2010). Second, in our model, all native forest is converted to sugar cane whereas it was also cleared to accommodate the growing population for settlements and for planting food crops. Regarding urban areas, approximately 5.5-9% of the present-day land area is occupied by manmade structures such as buildings, roads, etc. (Nigel et al. 2014, Hammond et al. 2015). Because the growth of urban areas throughout history is not accurately known, these areas are not included in the analysis, the only exception being the city of Port Louis. Soil loss under urban areas is usually considered to be zero (Nigel and Rughooputh 2010, 2012), although it might lead to increased runoff downstream. In addition, the soil protection of urban areas in the past was probably lower than today because it had less impervious surfaces. Ignoring most of the urban growth will likely lead to an overestimation of soil loss. Regarding food crops, the modeled soil loss will likely be underestimated because soil loss under vegetable crops is generally higher than under sugar cane (Le Roux et al. 2005, Nigel and Rughooputh 2012). From the 18th century onward, tea plantations were established in the wet uplands that were unsuitable for sugar cane. However, for most of the time, the crop only covered a small part of the island; until the 1960s, never more than 1.5% (Brookfield 1959). Today, tea covers 0.4–1.6% of the total land surface (Nigel et al. 2014, Statistics Mauritius 2014). Tea plantations have a lower erosion risk than sugar cane and vegetables because they are not periodically denuded at harvest (Nigel and Rughooputh 2010, 2012). Third, reforestation and establishment of timber plantations are not included in the analysis. Between 1880 and 1900, 1,600 ha (0.9% of total land surface) were planted with fast-growing tree species by the Forest Department (Brouard 1963). Timber plantations of mainly Loblolly Pine (Pinus taeda) were established in 1914, and large scale Slash Pine (Pinus elliottii) plantations were established from 1932 onward (Brouard 1963). From 1950 to 1959, 200–400 ha (approximately 0.1–0.2% of the island) were planted annually with fast-growing species such as Eucalyptus (Eucalyptus robusta, E. kirtoniana, and E. tereticornis), pine trees (Pinus elliottii and P. taeda), and Araucaria (Araucaria cunninghamii). Today, 25.3% of the island is covered with “forests, shrubs and

grazing lands" (Statistics Mauritius 2014), of which less than 2% consists of native forest (Florens 2013). The reason for not including nonnative forests and timber plantations in our analysis is that their exact location through time is not accurately known. Timber plantations do not provide the same soil protection as native forests because the trees are harvested every 7–10 years, when considering fast-growing tree species. It is often considered that 3 years after harvesting, the protective cover of timber plantations is comparable to that of a native forest (Lu et al. 2003). However, timber plantations have a much lower resistance than native forest to the heavy rains associated with cyclones that are common on Mauritius (Brouard 1963), increasing their erosion risk. Although soil disturbance under timber plantations is generally higher than native forest, it is lower than sugar cane because it has a longer cutting cycle. This leads to the fourth limitation: subannual and interannual changes in vegetation cover are not considered. Sugar cane is harvested annually by cutting the crop at ground level, after which the soil is left relatively bare before the crop has fully regrown again (Mardamootoo et al. 2013). Once every 7–8 years on average, the cane is replanted, for which the soil has to be tilled as well. The perennial character of sugar cane reduces erosion susceptibility under sugar cane compared with annually harvested crops (Mardamootoo et al. 2015). Although the practice of leaving crop residues on the field after harvesting is common, preharvest cane burning is still practiced as well, leaving the soil exposed and enhancing erosion. This relates to the fifth limitation: the support practice factor and cover management factor in the RUSLE are taken to be constant for a specific land-use type. As a result, differences between land owners (small vs. large growers) and related differences in sugar cane cultivation practices (e.g., manual vs. mechanized production) are not considered, whereas these may lead to differential landscape outcomes (Steen-Adams et al. 2015). During the first centuries of settlement, all sugar cane fields were harvested and planted manually. Today, large estates have mechanized their production process, but most small growers still do the planting and harvesting by hand. Throughout history, small growers often cultivated lands of inferior quality and produced less efficiently and less intensively compared with large growers (Brookfield 1959), which might lead to lower soil loss. Finally, the historical variation in precipitation and soil erodibility is not accurately known for the timescale of our analysis. Therefore, precipitation data for a 30-year time period was used to model soil loss. Soil erodibility based on a present-day soil map is used, although soil parameters, such as carbon content, soil thickness, and soil type are not static. In our model, soil formation and soil thickness are not considered, which might result in an overestimation of soil loss.

RESULTS

The influence of historical deforestation on soil loss in the different timeslices is clearly visible (Figure 4). In 1638, when the entire island was covered by native forest, the modeled soil loss values for nearly the entire island are within the lowest modeled soil loss class (0–2 t/ha/yr; Figure 4). As native forest is being converted to sugar cane in subsequent timeslices (1773, 1835, 1872, 1935, and 1997), several locations within the island fall within the moderate (2–12.5 t/ha/yr) and high (>12.5 t/ha/yr) modeled soil loss classes (Figure 4). In 1997 (Figure 4), areas in the center and northeastern parts of the island show high modeled soil loss values. These areas are characterized by the highest amounts of annual precipitation (Figure 1). Most lowland coastal zones and the western and northwestern part of the island have low rainfall values and low slope angles, which results in low to moderate modeled soil loss values.

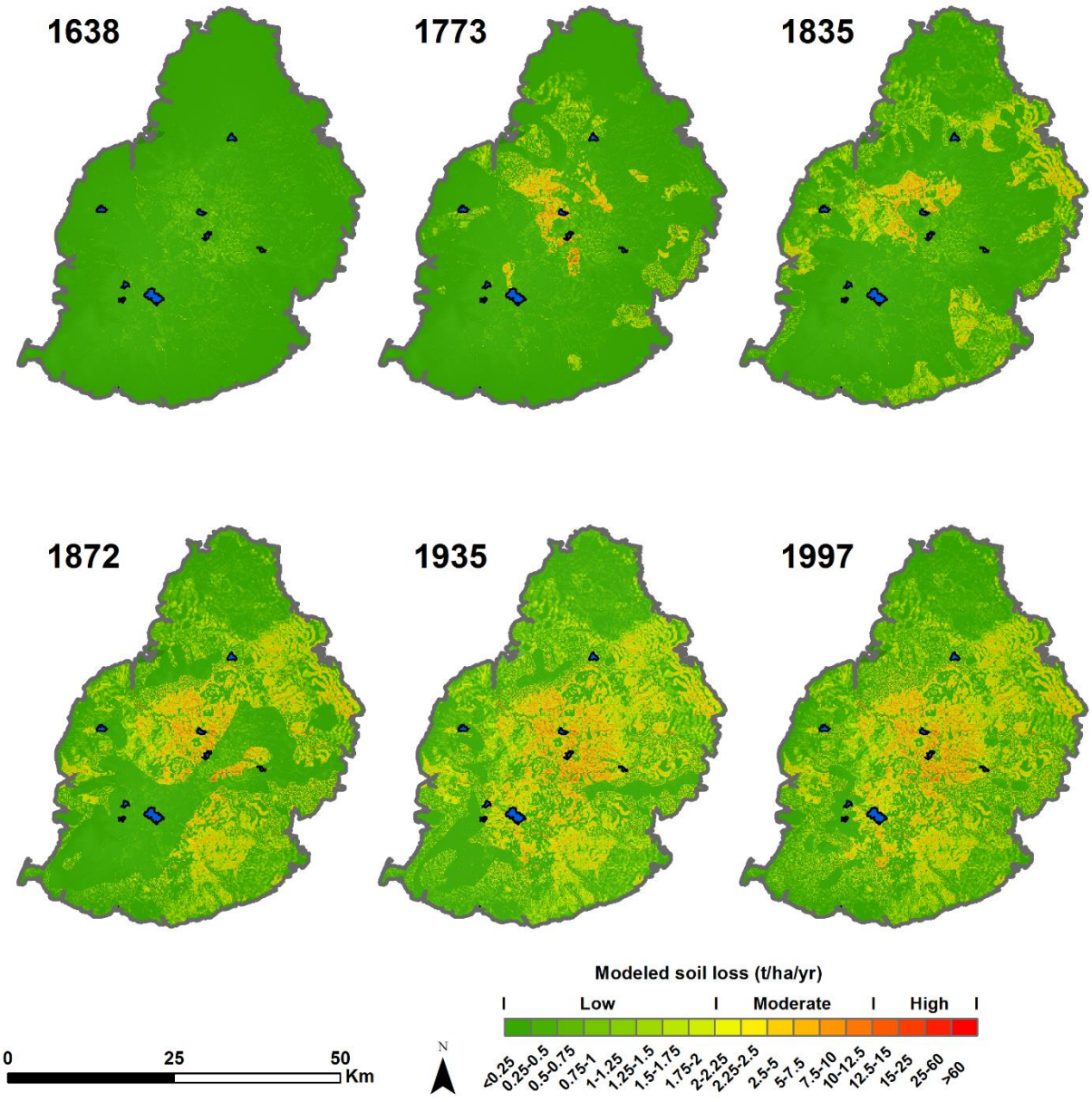

Figure 4. *Modeled soil loss for six timeslices since colonization in 1638. For visualization purposes, the modeled soil loss has been classified into three classes: low (0–2 t/ha/yr), moderate (2–12.5 t/ha/yr), high (>12.5 t/ha/yr).*

The maximum modeled soil loss for the 1638 timeslice with full native forest cover is 5.7 t/ha/yr (see upper graph of Figure 5). When assuming a bulk density of 1,200 kg/m3 (Montgomery 2007, Nigel and Rughooputh 2012), it can be calculated that this maximum modeled soil loss value under native forest is equivalent to a soil loss of 0.47 mm/yr. Between 1835 and 1935, wet areas on the central plateau with high annual rainfall were deforested, which generated high modeled soil loss, with a maximum of 61.4 t/ha/yr in 1935, equating to a soil loss of 5.1 mm/yr (assuming a bulk density of 1,200 kg/m3). It is clear that monthly

precipitation and modeled monthly soil loss per hectare are closely related (Figure 5, lower graph). The graph shows that seasonal variability in rainfall drastically influences the magnitude of modeled soil loss in different months. As a result, months with extreme precipitation have a prominent influence on the modeled annual soil loss.

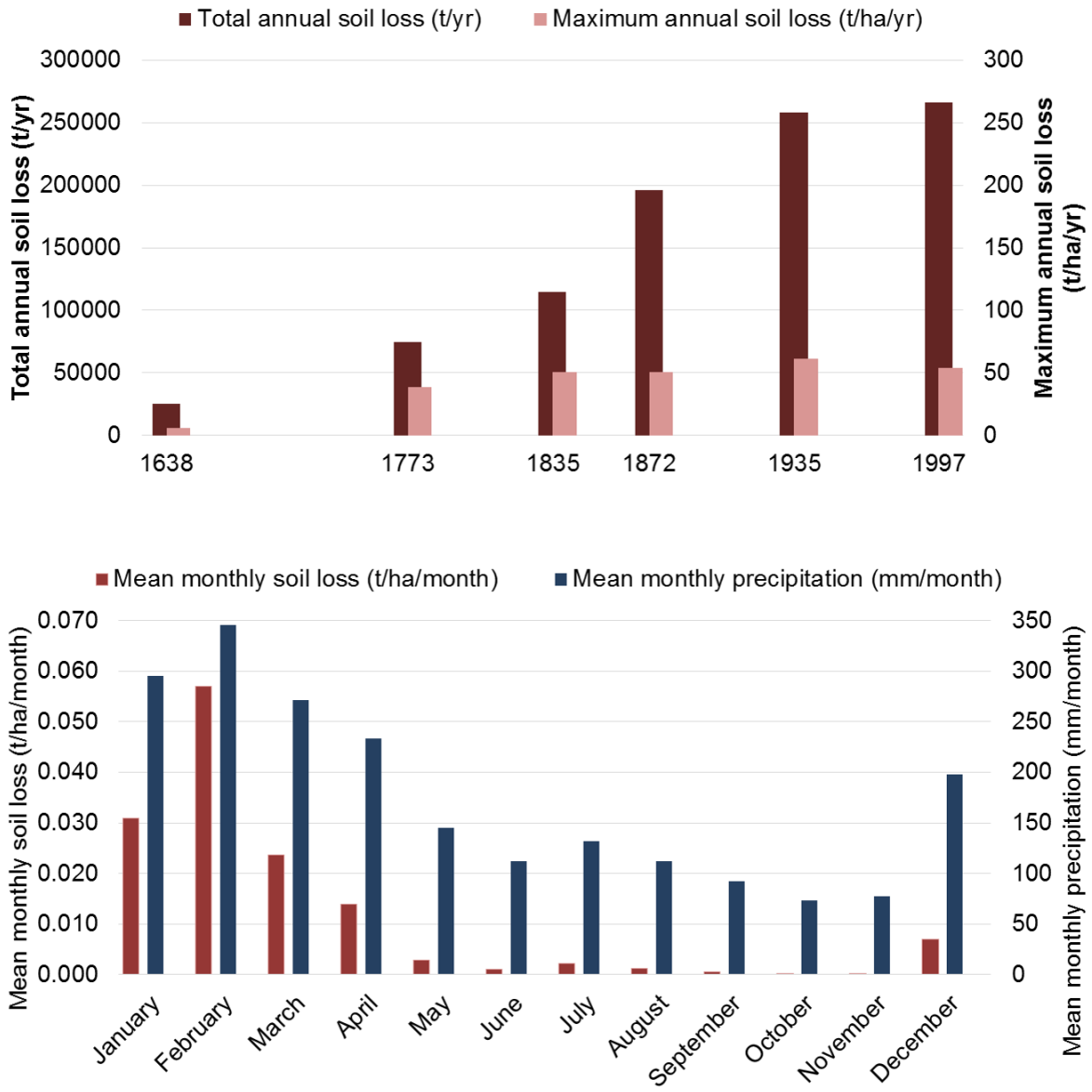

Figure 5. *Total annual modeled soil loss for the whole island (t/yr) and maximum value of modeled annual soil loss within the whole island (t/ha/yr) for each of the six analyzed timeslices (upper graph) and mean monthly modeled soil loss (t/ha/month) for the 1638 timeslice and mean monthly precipitation (mm/month, lower graph).*

Based on the modeled annual soil loss in the six timeslices (Figure 5, upper graph), the cumulative soil loss since the year 1638 for the whole island is reconstructed for two scenarios (Figure 6). In the scenario without deforestation, the cumulative modeled soil loss until the year 1997 is 9.2 million tonnes (green line in Figure 6). In the scenario with

deforestation, the cumulative soil loss increased drastically during the various stages of deforestation on Mauritius (orange line in Figure 6) up to a total soil loss of 49.1 million tonnes in 1997. Between 1638 and 1773, the percentage of native forest decreased to 82.5% of the original cover. In 1773, the cumulative soil loss was already twice as high compared with the baseline scenario. By 1835, when almost half of the island was deforested, cumulative soil loss was 2.5 times higher than the baseline scenario. The cumulative soil loss increases more rapidly in the second part of the 19th century. By 1872, when approximately 75% of the island had been deforested, the cumulative soil loss exceeded the baseline scenario by a factor of 3.1. As the felling of native forest continued, the cumulative modeled soil loss in 1935 and 1997 exceeds the baseline scenario by a factor of 4.3 and 5.4, respectively.

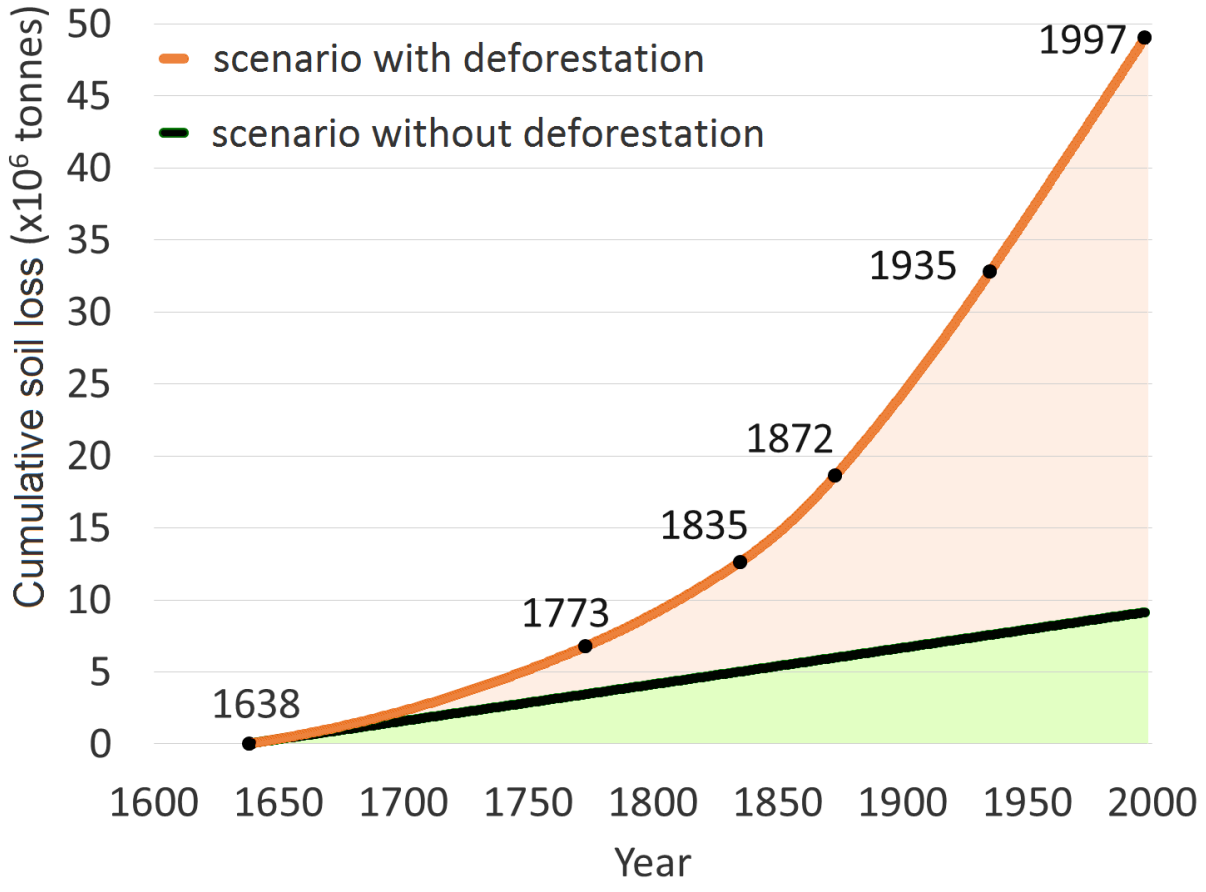

Figure 6. Cumulative modeled soil loss on Mauritius for a scenario with and without deforestation. To calculate cumulative soil loss for the scenario without deforestation, the soil loss in 1638 was used as the annual soil loss rate. In the scenario with deforestation, linear interpolation was used to reconstruct soil loss rates for the intermediate years between the modeled timeslices.

DISCUSSION

Temporal couplings

The cumulative soil loss scenarios provide an approximation of human impact relative to natural baseline erosion rates. Because of the limited detail and availability of historical data, some generalizations were necessary. Short-term fluctuations and the effect of extreme events are averaged out. However, such generalizations are inescapable for any study in which past human–environment interactions are modeled (Dearing et al. 2006, Fitzpatrick and Keegan 2007). Despite these generalizations, historical deforestation on soil loss over a period of nearly four centuries show some interesting patterns. Until the end of the 18th century, deforestation was limited to the easily accessible locations and areas close to the harbors. As a result, modeled soil loss during these early stages of deforestation was low. Deforestation and modeled soil loss started to accelerate in the first half of the 19th century when Mauritius was being transformed into a plantation economy. The general pattern that emerges on Mauritius shows that modeled soil loss increases over time and was highest during the most recent stages of deforestation. This temporal trend in soil loss is typical for the historical development of human impact on island ecosystems and environments, which starts gradually after initial colonization and accelerates as human populations grow and land use increases and intensifies (Rick et al. 2013). On Mauritius, during initial human settlement, lower fertile coastal regions were exploited first, whereas the less fertile higher grounds—especially those on steeper slopes—were exploited more recently. This might reflect a more general pattern on islands where settlements are mostly concentrated in lowland zones and high and steep areas are not permanently inhabited (Kirch 2007). Modeled soil loss resulting from deforestation drastically exceeds the natural variation in soil loss, leading to a growing soil debt. The soil debt only provides a general indication of how ecosystem services are influenced by deforestation. Our analysis does not show local details related to deforestation and soil loss. For example, actual impact of soil loss on provisioning services is closely related to the loss of topsoil, which typically has a higher fertility (Pimentel et al. 1995). Therefore, an initial erosion event in a certain locality has stronger impact on fertility than a younger erosion event under similar conditions. Although time lags can exist before the impacts of historical land-use change and deforestation become visible (Foster et al. 2003, DeFries et al. 2004), historical sources show that the impact of deforestation on soil fertility and droughts on Mauritius were already recognized during the 18th and 19th centuries (Brouard 1963, Grove

1996). For example, in a government report dating from 1870, it is mentioned that "large-scale soil denudation has continued the work of destruction by deforestation. [...] Finally, the fertility of soils has been greatly affected" (Régnaud 1870 quoted in Brouard 1963). In recent years, 36% of the soils had a phosphorus deficiency (Mardamootoo et al. 2010), and average yield of sugar cane per hectare has been declining during the last decades (Umrit et al. 2014, Cheong and Umrit 2015). These findings agree with a study on Hawaii, where nearly four centuries of agricultural practices have significantly reduced soil fertility (Kirch 2007). On Mauritius, loss of soil fertility does not seem to be among the major causes of land abandonment; small planters that leave their land fallow, or shift from sugar cane to vegetable cultivation, are mainly motivated by social–economic factors (Lalljee and Facknath 2008). Aside from the loss in soil fertility, several other ecosystem services are impacted by soil loss. Soil loss leads to increased water runoff, lower infiltration rates, and lower water-holding capacity (Pimentel et al. 1995), which can affect vegetation growth. Offsite effects of erosion processes include siltation, loss of reservoir storage, and increased water treatment costs (Pimentel et al. 1995). These aspects are especially relevant for Mauritius given the island's chronic water scarcity (Ramjeawon 1994) and its 74% dependency on external water resources (Hoekstra and Mekonnen 2012). These important impacts strongly suggest that the capacity of the soil to provide ecosystem services has been undermined.

Historical soil loss mitigation

Raudsepp-Hearne et al. (2010) raised the question why human well-being is increasing, while ecosystem services are degrading on a global scale. The analysis of temporal- and telecouplings on Mauritius provides an interesting perspective on how this apparent paradox is expressed on a local scale. Despite the negative impacts of historical deforestation and soil loss on ecosystem services, Mauritius is generally considered a success story considering its sustained economic growth and the well-being of its inhabitants (Sobhee 2009, Bunwaree 2014), although not all segments of the population benefited equally (Bunwaree 2014). Between 1980 and 2013, the human development index (HDI) of Mauritius has been increasing gradually; today, Mauritius holds the 63rd position of 187 countries and territories (United Nations Development Programme 2014). This seems to coincide with a decreasing dependency of the Mauritian economy on locally provided ecosystem services. Today, agriculture (including sugar), forestry, and fishing contribute only 3% to the gross domestic product (GDP), and the manufacturing of, respectively, foodstuffs and sugar contributes an additional 6.1% and 0.2% (Mauritius Chamber of Commerce and Industry 2015). Globally,

land becomes an increasingly scarce resource, which leads to growing competition between different land uses (Lambin and Meyfroidt 2011). On the island of Mauritius, where all land is allocated and is scarce, three out of the four major Mauritian sugar cane companies have invested in property on the African continent (http://www.omnicane.com/, http://www.alteogroup.com/, http://www.terra.co.mu/). The latter illustrates that land-use change on islands cannot be understood in isolation, as Baldacchino (2004) rightfully notes, "Islands are not islands, in the sense that they are not closed unto themselves." Since its colonization, Mauritius always held strong links and dependencies with other localities (Eriksen 1993), through its dependency on slave labor, its imports of food and fertilizer, and for a long time, its sugar exports. It seems that throughout history, the negative impacts of deforestation and soil loss have been partly offset by a strong dependency on trade in global markets. For example, in the 1950s, 30% of the sugarcane lands on Mauritius had a phosphorus deficiency, after which phosphorus imports increased tenfold between 1955 and 1970 (Mardamootoo et al. 2010). Although the capacity of the soil to provide ecosystem services to society has been undermined as a result of temporal couplings, negative impact on the SES of Mauritius seems to be partly mitigated by telecouplings with other SES. However, a heavy reliance on fossil energy and fertilizer imports to mitigate the consequences of soil loss can likely not be sustained over the long term (Pimentel et al. 1995) and has both economic and environmental costs. Mitigating the impacts of soil loss by increasing the use of fertilizers can negatively influence other ecosystem services. On Mauritius, high phosphorus and nitrogen concentrations in runoff waters have been recorded (Ng Kee Kwong et al. 2002), leading to eutrophication in the coastal zone (Ramessur 2002), which might in turn negatively impact coastal fisheries and tourism. In addition, 50% of the energy consumption involved in sugar production on Mauritius is taken up by fertilizers (Ramjeawon 2004). Finally, fossil energy and phosphate rock, which are both used for fertilizer production, are finite (Cordell et al. 2009), which further stresses the need for Mauritius to pay back the soil debt. While paying this debt, those localities with highest soil erodibility should receive high soil conservation priority and, during periods of heavy rainfall, vegetation cover should be ensured (Nigel and Rughooputh 2010, 2012). Moreover, restoration approaches should take into account the degree to which the soil has already been degraded by temporal couplings such as historical land use and deforestation.

CONCLUSION

Our objective was to study the effects of temporal couplings on the current state of a SES. We operationalized these temporal couplings by focusing on the influence of historical deforestation on cumulative soil loss on Mauritius. Based on historical deforestation maps, we modeled soil loss for six timeslices since human colonization of Mauritius in 1638. We have compared the soil loss resulting from deforestation to a baseline scenario in which the entire island remained covered by forest.

We conclude that deforestation has led to a drastic increase in soil loss since first human settlement. Cumulative soil loss resulting from deforestation exceeds the natural soil loss baseline by more than five times. Such a soil loss is not sustainable over the long term when assuming soil formation rates to be in equilibrium with soil loss under native vegetation. It is further concluded that the cumulative soil loss undermines the capacity of ecosystems to provide services to society today and in the future, but that the negative consequences of soil loss are partly mitigated by telecouplings with SES abroad. The latter underpins that islands, as any locality, cannot be understood in isolation and that connections with other SES should be taken into account. Future research on insular SES should address that the current state of a SES emerges from the interaction between temporal couplings and telecouplings.

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2.2 Global change in microcosms: environmental and societal predictors of land cover change on the Atlantic Ocean Islands

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SJN conceived and coordinated the research, largely developed the workflow, analysed the data, and wrote the manuscript. Co-authors contributed data, revised the manuscript and participated actively in discussions about interpretation of the results.

ABSTRACT

Islands contribute enormously to global biodiversity, but their species and ecosystems are highly threatened and often confined to small patches of remaining native vegetation. Islands are thus ideal microcosms to study the local dimensions of global change. However, while all islands have been drastically transformed by human activities, it remains unclear to which extent differences in land cover between islands are shaped by societal and environmental conditions. Here, we analyze the role of contrasting environmental and societal island contexts in affecting the extent of native vegetation cover on 30 islands in five Atlantic archipelagos. We adopt a mixed-method approach in which we combine a statistical analysis of environmental and societal variables with a qualitative reconstruction of historical socioeconomic trends. Our statistical results indicate that the extent of native vegetation cover is predominantly shaped by terrain ruggedness, suggesting that human impacts on biodiversity are influenced by topography. Overall, differences in native vegetation cover between islands were better explained by environmental variables than by societal variables like human population density. However, throughout history, islands experienced large changes in demography and socioeconomic trends, and therefore current patterns of native vegetation might also partly reflect these past conditions. While anthropocene narratives often present humans as a global geophysical force, human impacts on biodiversity at the local scale are strongly modified by the local environmental context. We urge for integrative approaches to understand the main contributions of local human-environment interactions to ongoing global change.

Key words: Land use land cover change; global biodiversity change; social-ecological systems; Macaronesian Islands; topographic ruggedness; qualitative-quantitative mixed-methods

INTRODUCTION

Land use change and biodiversity loss

Following human settlement of previously uninhabited lands, native vegetation cover has been converted to agricultural and other land uses, reducing and fragmenting the habitat of many native species (Boivin et al., 2016; Nogué et al., 2017), contributing to the extinction of species and degredation of communities. By understanding the drivers of land cover change, we might better predict which areas have a high risk of being converted, and where this coincides with high native and endemic biodiversity. However, global scale studies on land cover change have focused almost exclusively on changes in forest cover (Lambin and Meyfroidt, 2011; Meyfroidt et al., 2010; Rudel et al., 2005), often disregarding the differences between native and exotic-dominated forests and the ecological value of non-forest ecosystems (Tropek et al., 2014). While it is clear that present-day native vegetation cover is the outcome of both environmental and societal factors, the study of their relative importance and interactions is rarely integrated. This is partly due to contrasting methodological approaches across the social and natural sciences (Magliocca et al., 2018), which tend to attribute *a priori* relevance to a limited set of factors. On the one hand, approaches that synthesize a large number of qualitative case-studies have emphasized the potential role of economic, institutional, technological, cultural, and demographic variables in land use change but overlook topographic and climatic variables (Geist and Lambin, 2006; Lambin et al., 2001). On the other hand, quantitative studies that rely on statistical models have shown the importance of environmental variables (Rolett and Diamond, 2004; Sandel and Svenning, 2013), but often do not consider contrasting regional contexts and historical trends. Hence, there is a need for interdisciplinary approaches that analyze environmental and societal aspects in their regional and historical context (Biermann et al., 2016; Brondizio et al., 2016; Costanza et al., 2007; Dearing et al., 2015; Haldon et al., 2018; Kotchen and Young, 2007).

Islands are ideal model systems for studying local human-environment interactions within their regional and historical context because of their clearly defined boundaries, relative isolation, and clear onset of human settlement (Dinapoli and Leppard, 2018; Kirch, 1997; Russell and Kueffer, 2019; Vitousek, 2002; Warren et al., 2015). Furthermore, islands deserve particular attention in light of global change because they are disproportionally affected by the current biodiversity crisis. Although islands make up less than 8% of the global land surface (Sayre et al., 2018), more than 60% of known extinctions were island species (Tershy et al.,

2015; Whittaker et al., 2017). Moreover, the remaining island biodiversity is disproportionally threatened (Cardillo et al., 2006; Ricketts et al., 2005): 41% of all globally endangered terrestrial vertebrates live on islands (Spatz et al., 2017). Crucial is that much of the biodiversity on islands is contained within remaining patches of native vegetation. The disappearance of native vegetation cover – together with the impact of invasive species and overexploitation – is a major cause of biodiversity loss on islands (Braje and Erlandson, 2013a; Fordham and Brook, 2010; Graham et al., 2017; Wood et al., 2017). While the impact of land use/land cover on biodiversity is higher on islands than on mainlands (Kier et al., 2009; Sanchez-Ortiz et al., 2019) and native vegetation cover across islands worldwide has been vastly reduced following human colonization, it is still not fully understood why some islands are more affected than others. Both environmental factors and human intervention are possible sources of such variation, but what is the relative importance of environmental versus societal contexts in explaining differences in native vegetation cover across islands? It could be that certain island societies have a larger impact, or that environmental conditions on some islands increase the likeliness of native vegetation cover to be reduced. Here, we test these hypotheses by analyzing the impact of both environmental and societal factors in shaping native vegetation cover on 30 oceanic islands across five archipelagos in the Eastern Atlantic: Azores, Madeira, Canary Islands, Cape Verde (i.e. the Macaronesian Islands), and Gulf of Guinea Islands (Figure 1).

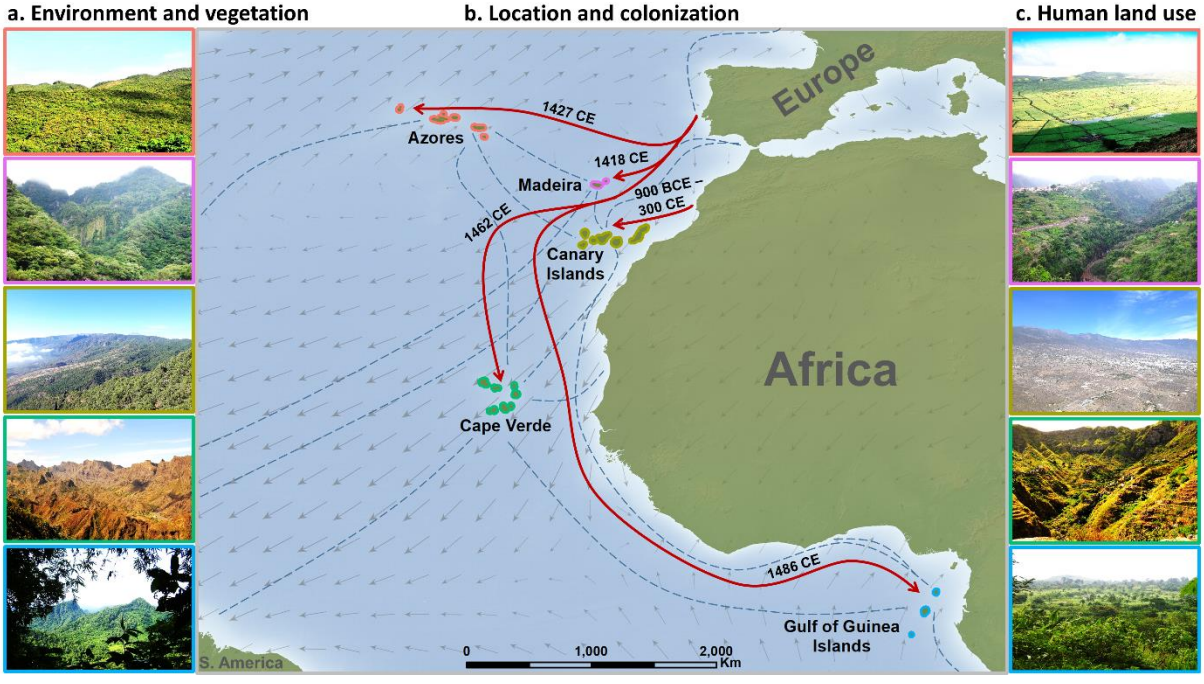

Figure 1. Contrasting environmental and societal conditions, and location of 30 Eastern Atlantic Islands within five Archipelagos (Azores, Madeira, Canary Islands, Cape Verde, Gulf of Guinea Islands) off the coasts of

Africa and southern Europe. a) Environmental context and vegetation cover of the five archipelagos. For each archipelago we selected one island as an example (from top to bottom: Terceira for the Azores, Madeira Island for Madeira, Tenerife for the Canary Islands, Santo Antão for Cape Verde, and São Tomé for the Gulf of Guinea Islands). b) Location of the archipelagos, their colonization history and trade connections. Red arrows indicate the year of human settlement and approximate colonization route. The Canary Islands were first colonized from northwest Africa (Fregel et al., 2019; Navarro, 1997), the remaining archipelagos were initially colonized from the Iberian Peninsula (Fernández-Palacios et al., 2016a). Blue stippled lines indicate historical connections between different localities (travel, trade, transport), illustrating that the Eastern Atlantic Islands were at the nexus of the emerging transatlantic trade networks. Grey arrows indicate wind direction and speed; although ocean currents and wind regimes may have shifted over much longer timescales (Fernández-Palacios et al., 2016b), for the period considered here the direction of the trade winds was similar to the present-day (Dartnell, 2018). Wind direction and speed in panel b were calculated with R (version 3.5.3) (R Core Team, 2019) from data on long-term monthly means of the u and v component (obtained from https://www.esrl.noaa.gov/). CE = Common Era, BCE = Before Common Era. c) Differences in human land use across the archipelagos (islands are the same as in panel a). Although prior to the 15th century, the Atlantic had been extensively navigated by the Vikings (Dugmore et al., 2012), who possibly colonized some of the Eastern Atlantic Islands (Gabriel et al., 2015), we did not consider this due to the uncertainty in the onset and impact of possible Viking settlements. All photos in panel A and C were taken by the authors.

The human-environment interactions that evolved on the Eastern Atlantic islands were microcosmic experiments that shaped subsequent interactions in other islands and in mainland locations across the globe (Crosby, 1984; Moore, 2015). This is illustrated by the global history of sugar, for example, whereby the islands acted as testing grounds for sugar colonies that were later established in the Caribbean, Brazil and elsewhere around the world (Galloway, 1989; Mann, 2011; Mintz, 1986). Of the five archipelagos included in this study only the Canary Islands had a human population when Europeans arrived in the 15th century. The conquest of these islands by the Castilians started in 1402 and decimated the native population (Crosby, 1984). While the native population of the Canary Islands had a notable impact on the islands (Morales et al., 2009), the conquest of these islands and colonization of the previously uninhabited Eastern Atlantic Islands by Europeans in the 15th century caused further transformations of the islands' landscapes and ecosystems (Fernández-Palacios et al., 2016a). During the Age of Exploration (early 15th century to mid-17th century), these islands became stepping stones in emerging maritime trade routes, and facilitated the transport of plants, people, and materials between Europe, the Americas, Africa, and Asia (Crosby, 1972). Despite their pivotal role in propelling human-induced changes to a global scale, these islands have not received much attention as microcosms of global change.

MATERIAL AND METHODS

Island-level data on environment and society

To test the relative importance of environmental and human drivers of native vegetation cover across islands, we considered several topographic, climatic, and societal variables. As proxies for island topography, we compiled data on island area (km^2) and maximum elevation (m), and calculated the island-level mean of the Terrain Ruggedness Index (Riley et al., 1999) from NASA Shuttle Radar Topography Mission (SRTM) data. Void filled data were downloaded from the United States Geological Survey (https://earthexplorer.usgs.gov/) at the highest available resolution (1-arcsecond, or approximately 30 meters). While island topography is constantly changing as a result of geomorphological processes like volcanic eruptions and erosion, the effect of these processes on island-wide topography is negligible at the timescale of centuries considered here. For climate, we used the long-term annual mean temperature (°C) and precipitation (mm/year) from the WorldClim 2 database (http://worldclim.org/version2) (Fick and Hijmans, 2017), calculated over the period 1970-2000 (see map in Fig A.1 for Köppen-Geiger classification per archipelago). While climate fluctuations between 1500 and 1800 had serious repercussions for socioeconomic developments in continental Europe (Zhang et al., 2011), their impact was likely smaller on the Eastern Atlantic islands, thanks to the buffering effect of the surrounding ocean (Cronk, 1997). In addition, while temperatures in the Eastern Atlantic were approximately 3 °C lower during the Little Ice Age (1400-1700 CE) compared to recent years, the anomalies are relatively consistent across the islands considered here (Mann et al., 2009). Therefore, using modern topographic and climatic variables for understanding human-environment interactions over the last centuries will not change patterns across islands.

As potential societal drivers of native vegetation cover, we included modern population density and used an index of human landscape modification (Kennedy et al., 2019). Average population densities were calculated by dividing modern human population size (see Table A.1 for sources) by island area. The index of human landscape modification was obtained from a global spatially explicit dataset on cumulative human modification of terrestrial lands at $1km^2$ resolution (Kennedy et al., 2019). The index is based on spatial patterns of human settlement, agriculture, transportation, mining, energy production, and electrical infrastructure (Kennedy et al., 2019). Calculating the island-level mean from this database therefore reflects both the extent and intensity to which the landscape of a particular island is transformed by

human activities. Data preprocessing for these quantitative variables was performed with R (version 3.5.3) (R Core Team, 2019). The full dataset is provided in Table A.2.

Island-level data on native vegetation cover

We defined native vegetation cover as the total land area of an island that is predominantly covered by native plants (species that were present on the islands prior to human arrival). Total native vegetation cover can therefore include both forest and non-forest vegetation, and can consist of primary as well as secondary vegetation. Introduced plants are widespread across all Eastern Atlantic Islands (Castro et al., 2010; Jardim and Menezes de Sequeira, 2008) and it can be challenging to determine the chorological status for individual species (van Leeuwen et al., 2008). Therefore, we compiled data on native vegetation cover for each island from different sources. For islands that had land use/land cover maps available, the extent of native vegetation was assumed to be delimited by areas labelled as 'native vegetation' or 'natural vegetation'. In other cases, we had to determine which labels most closely matched the definition. For the Azores we used the area classified as 'natural vegetation' from the land cover map of the regional council (Secretaria Regional do Ambiente e do Mar, 2007). This category includes secondary forests and non-forest areas that largely consist of native species but also grasslands that are relatively poor in terms of native communities. As a consequence, the map for the Azores likely overestimates native vegetation cover (Connor et al., 2012). To see if this would affect our results, we re-ran our analyses with an alternate, more conservative definition of native vegetation for the Azores, where only the extent of remnant patches of native forest was included (Gaspar et al., 2011). For Madeira, we obtained data from the European Nature Information System database (European Environment Agency, 2018), which included a mix of vegetation types consisting of native shrubs and secondary vegetation, but also contained an unknown percentage of exotic vegetation. For the Canary Islands, we summed the total cover of the areas classified as 'actual natural vegetation' (Table 1 in del Arco Aguilar et al., 2010), which included secondary vegetation types. We did not include: nitrophilous herb communities, of which the spread is mainly a result of grazing (del Arco Aguilar et al., 2010), secondary vegetation with a high proportion of exotic species, or plantations of Canary pine. For Cape Verde, we digitized maps of the agro-ecological zones per island (Diniz and de Matos, 1999, 1994, 1993, 1988, 1987, 1986) and made an overlay with a global land use land cover map (ESA, 2017) in a Geographic Information System (ArcGIS version 10.6.1). The resulting maps were classified into different land use/land cover classes. Within the arid zones, grasses (Poaceae)

are most common in terms of species richness and we assumed that 50% of the vegetation cover in these zones is predominantly native. For the Gulf of Guinea Islands, data for São Tomé and Príncipe were obtained from Jones and Tye (2006) and sources therein; these data include both primary and secondary forest. For Annobón, we made an overlay of the island's vegetation map (Heras et al., 2002) and the land cover map of Equatorial Guinea (Ministerio de Agricultura y Bosques, 2013) to assess the percentage of native vegetation cover. To complement these quantitative data on native vegetation cover per island, we did a more in-depth qualitative assessment of the biodiversity changes during human contact (Table A.3), including the vegetation cover around the time of first human colonization as a reference point (Braje et al., 2017; Nogué et al., 2017) as well as the current biodiversity status of each archipelago.

Statistical Analyses

Using native vegetation cover as the response variable, we evaluated the relative importance of seven aforementioned environmental and societal variables: terrain ruggedness, island area, maximum elevation, mean annual temperature, mean annual precipitation, human landscape modification, and population density. We first calculated the variance inflation factors to assess collinearity among predictor variables, using a threshold value of 3 (Zuur et al., 2010). To understand how islands are clustered in terms of environmental and societal variables in relation to the response variable native vegetation cover, we did a partial least squares regression analysis (Frank and Friedman, 1993; Hastie et al., 2009). This method combines the principles of a principal component analysis and multiple linear regression to decompose the matrix of several predictor variables into components, or latent variables, that predict the response variable. The latent variables are formed such that these explain the maximum amount of variance in the response variable. The kernel algorithm (Dayal and Macgregor, 1997) was used to fit the model. A permutation approach was used to select the appropriate number of components in the model (Hastie et al., 2009). The partial least squares regression analysis was carried out using functions from the R-package pls (Mevik and Wehrens, 2007). To assess whether islands are clustered by archipelago in terms of environmental and societal variables (regardless of native vegetation cover), we plotted the results of a principal component analysis. Finally, to identify the most important environmental and societal variables that contributed to the response variable native vegetation cover, we did a multiple linear regression analysis using all seven predictor variables (the 'full model'). As a complementary approach to fitting the full model, we also followed a model averaging

approach. All statistical analyses were performed within the R statistical programming environment (version 3.5.3) (R Core Team, 2019).

Historic socioeconomic trends at the archipelago-level

The quantitative societal variables which we used in our statistical analyses represent modern conditions and can aid in discerning spatial patterns across islands. However, societal conditions on individual islands and archipelagos may have changed irregularly over time. For example, population density on some archipelagos during past periods may have been higher than today. Therefore, we compiled demographic data for each archipelago to explore historical fluctuations in population density (see Table A.1 for sources). Similarly, modern patterns of landscape modification are the ultimate outcome of historical human-environment interactions. To understand the historical context of the archipelagos, we made a qualitative reconstruction of past socioeconomic trends based on information from historical descriptions and academic articles. We placed emphasis on 1) the economic importance of agricultural production for local consumption within the archipelago, relative to 2) the export and trade of food crops, commodities, and slaves. For each archipelago this resulted in a summary of the main socioeconomic developments per century (see Tables A.4-A.8 in the appendix). To facilitate a comparison across archipelagos, we made a visualization of the main historical socioeconomic trends in each of them. We did this by scoring the relative importance of both categories on a scale ranging from ‘low’ to ‘high’. A century was divided in four sections of 25 years, and a score was assigned to the closest interval (e.g. if historical descriptions indicate a peak around the year 1506, we assigned a score between 1500 and 1525). These importance scores were subsequently plotted over time with a smooth line connecting the points. We added icons to the timeline to indicate major crops or activities (e.g. a peak in sugar cane production). These visualizations were made to gain insight in differences across archipelagos regarding the timing and direction of historical socioeconomic developments, not for a quantitative comparison in terms of the magnitude of events.

RESULTS

To assess the extent to which island-level socio-environmental variables shape present-day native vegetation cover we performed a partial least squares regression analysis (PLSR) by using variables related with topography (terrain ruggedness, island area, maximum elevation), climate (mean annual temperature and precipitation), and society (human landscape modification, population density). All variance inflation factors were below 3 (Table A.9),

suggesting that collinearity did not strongly affect the model. The first and second axes of the PLSR explain nearly 70% of the variation in native vegetation cover, of which more than 60% by the first axis alone, which is mainly correlated with terrain ruggedness and elevation (Figure 2). This suggests that native vegetation cover is more influenced by topographic conditions of individual islands than by societal and climatic variables. In addition, islands within an archipelago did not seem to be strongly clustered. A principal component analysis (PCA) of socio-environmental variables (without native vegetation cover) confirms this pattern: islands within the same archipelago are not strongly clustered along the first and second axes (Fig. A.2), but show some grouping along the third axis, mainly related to climatic differences (Fig. A.3).

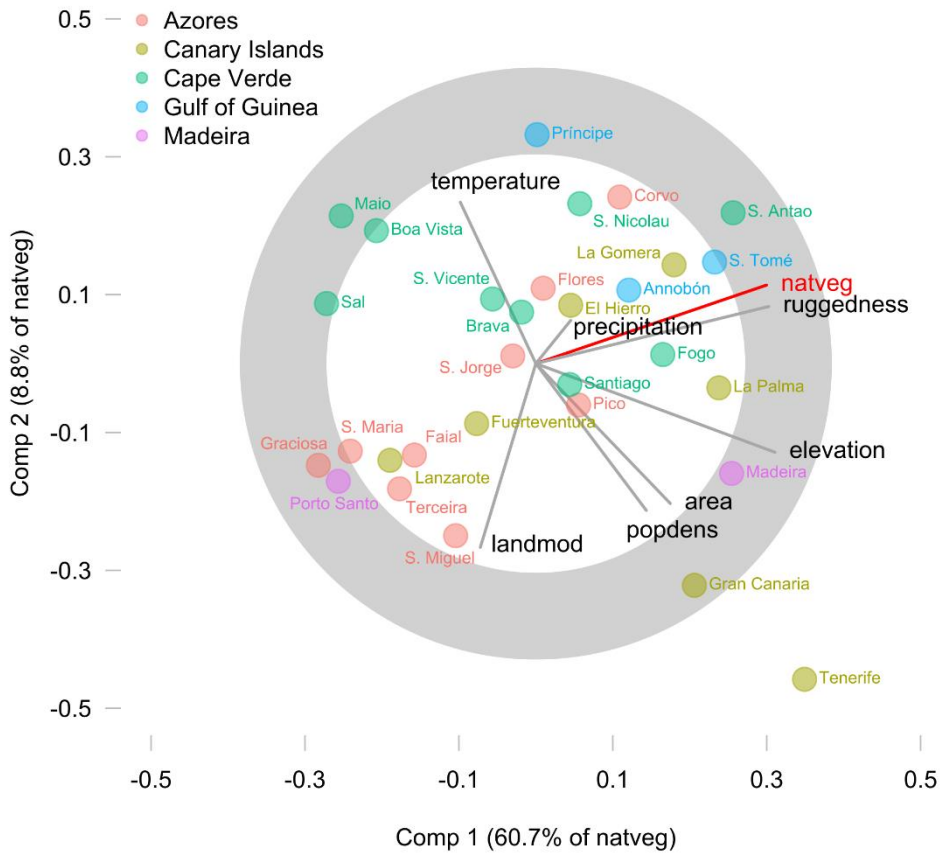

Figure 2. Covariation of topographic, climatic and societal variables, as obtained from the partial least squares regression analysis (see Methods), to explain variation in native vegetation cover (natveg) across the 30 Eastern Atlantic Islands. Latent variables are constructed based on variables related to topography (ruggedness, area, elevation), climate (temperature, precipitation), and society (human landscape modification, population density). The length of the grey lines is indicative of the importance of each predictor in constructing the latent

variables. The grey band indicates that the correlation of a predictor variable or the response variable with the first and second latent variable is higher than 50%. See Table A.10 for coefficients of the partial least square regression model.

To quantify the relative importance of environmental and societal conditions in shaping native vegetation cover, we fitted a multiple linear regression model consisting of seven topographic, climatic, and societal variables ('full model') using native vegetation cover on each island as the response variable. Differences in the extent of native vegetation cover are most strongly correlated with terrain ruggedness of islands (Figure 3a), explaining over 45% of the variance across the 30 Eastern Atlantic islands. In addition to terrain ruggedness, maximum elevation and degree of landscape modification also play a role. Island area and temperature also explained some of the variance, while the effect of population density and precipitation was negligible. The partial response of native vegetation cover to ruggedness, while controlling for the effect of other variables in the full model, highlights the importance of this key explanatory variable (Figure 3b). We ran additional analyses for a second dataset in which for the Azores we only considered native forest as native vegetation. While individual parameter values changed, the overall trends remained the same (Figure A.4). Finally, model averaging yielded comparable results to those of fitting the full model (Figure A.5).

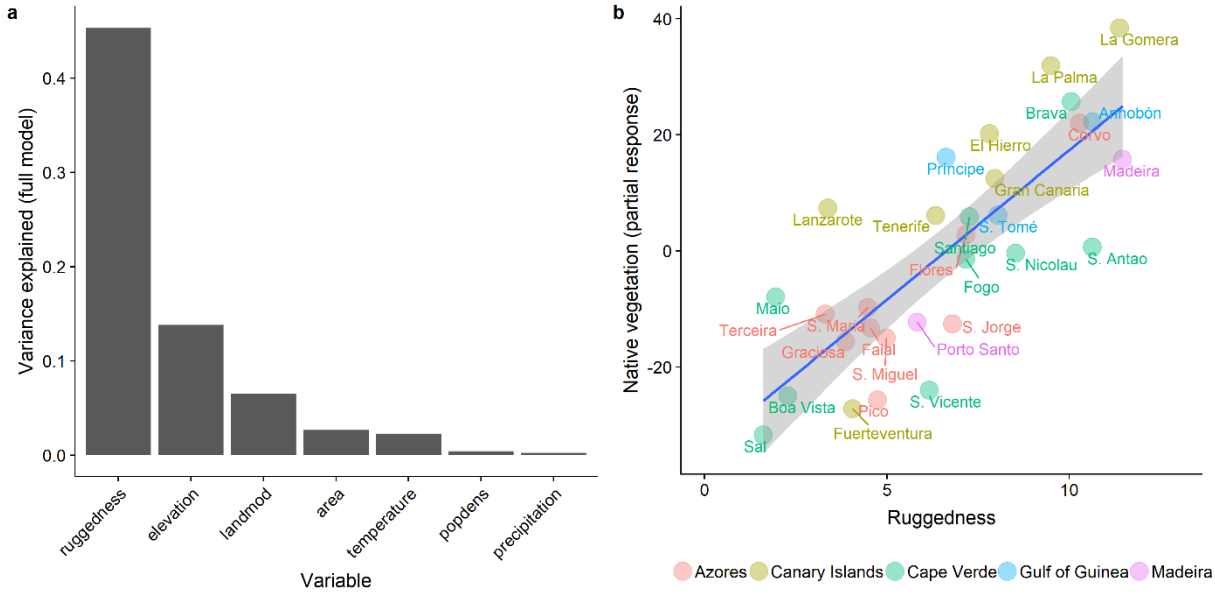

Figure 3. The effect of environmental and societal variables on native vegetation cover across 30 Eastern Atlantic Islands. Results were obtained by fitting a multiple linear regression model consisting of seven topographic, climatic and societal variables ('full model'), using native vegetation cover as a response. a) Contribution of each predictor in the full model to the explained variance in native vegetation cover. The full model could explain 71.3% (R^2) of the variance, 45.3% of which is explained by ruggedness alone. b) Partial

residual plot showing the relationship between ruggedness and the partial response of native vegetation cover in the full model.

In our statistical analyses, societal variables appear to be of lesser importance than topographic variables in shaping native vegetation cover. While human landscape modification had some influence, population density had a negligible effect. However, modern population density is not representative of the entire period since initial human settlement. While in some archipelagos human population density grew steadily, others witnessed steep fluctuations (Figure 4a). For most of the last five centuries population density of the Azores was higher than in the Canary Islands and Gulf of Guinea Islands, but this was reversed halfway the 20th century. In the Azores and Madeira population density is currently below its peak in the 20th century. In addition to these demographic changes we also find strong differences across archipelagos regarding their historical socioeconomic developments (Tables A.4-A.8; Fig. 4b-f). For example, sugar cane has been introduced to islands of all five archipelagos, but the extent to which the crop affected the local economy and environment differed. Sugar cane production was produced at a large scale especially in Madeira and later in the Gulf of Guinea Islands (Figure 4c,f; Tables A.5 and A.8). When the importance of sugar production dwindled in these archipelagos, the sugar cane commodity frontier moved away from the Eastern Atlantic to other parts of the world such as the Caribbean and Latin America (Galloway, 1989). Subsequently, the economies of Madeira and the Gulf of Guinea switched to other forms of income but kept their focus on exports, namely wine, slaves, coffee and cocoa. The socioeconomic histories of Madeira and the Gulf of Guinea contrast with that of the Azores, and to a lesser extent also that of the Canary Islands (Figure 4b,d; Tables A.4 and A.6), which likely retained a larger degree of food self-sufficiency. On Cape Verde, crop cultivation was of little importance and its economy was centered on activities that were less bound to the land, such as salt export, and commercial exchanges, being an important entrepôt for ship fueling and for the slave trade (Figure 4e; Table A.7).

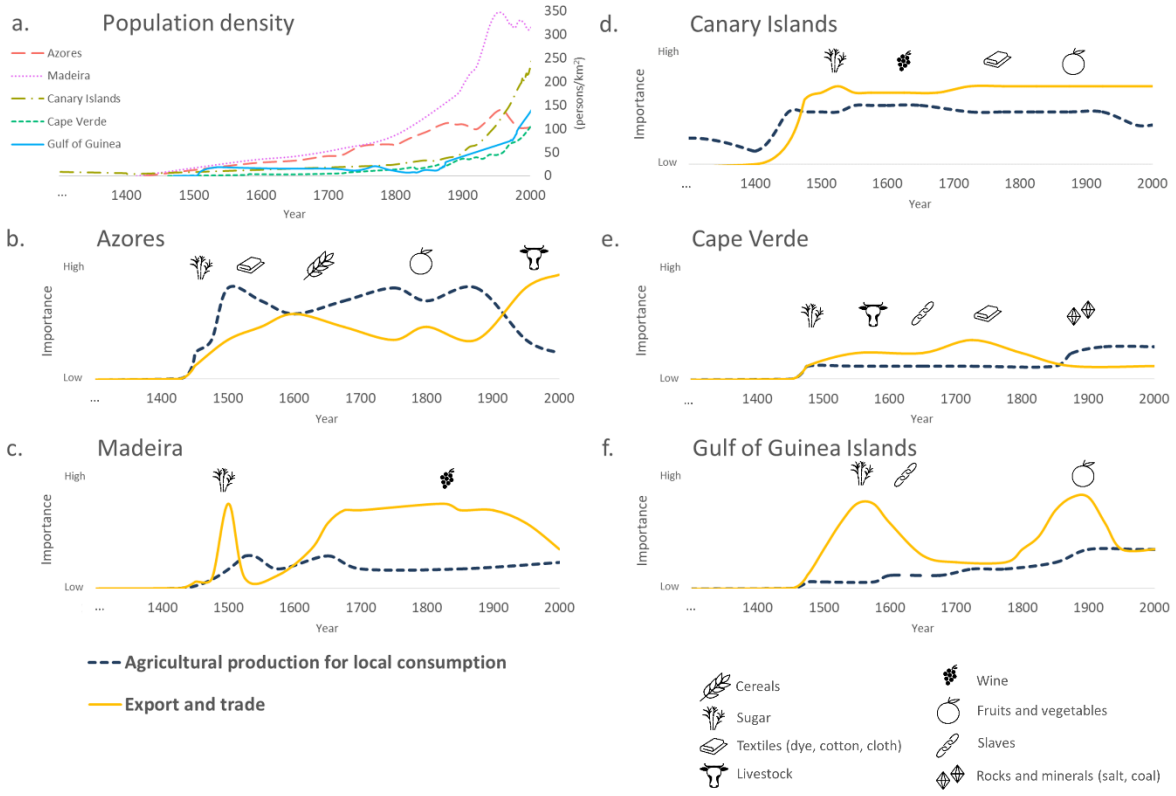

Figure 4. Historical socioeconomic and demographic changes in the Eastern Atlantic archipelagos (ordered from North to South). a) Changes in population density per archipelago. Population density was estimated from the sources in Table A.1; those years for which no census data were available were interpolated. b-f) Visualization of changes in export and trade, and in agricultural production for local consumption for each archipelago. The X-axes indicate the years (CE), while the Y-axes show the relative economic importance of agricultural production for local consumption, and of export and trade of food crops, commodities, and slaves. The visualizations are based on the historical descriptions in Tables A.4-A.8. The icons illustrate crops and events of major importance.

DISCUSSION

Island ruggedness, land use decisions and native vegetation

The aim of this study was to understand to what extent contrasting environmental and societal contexts explain differences in present-day native vegetation cover across islands in the Eastern Atlantic. The results of our statistical analyses indicate that environmental variables can explain a larger part of the variance in native vegetation cover across islands than societal factors. More specifically, terrain ruggedness, plays a key role in shaping native vegetation cover. A possible explanation for this observed relationship is that on rugged islands, people restrict land use to the more accessible – less rugged – areas. The fact that ruggedness holds an inverse relationship with human landscape modification lends further support to this

interpretation (Figure 4; Figure A.6). Our results are in line with Sandel and Svenning (2013) who found that topographic slope over large spatial scales (500 m – 32 km) drives human impact on tree cover globally. While ruggedness and slope represent different aspects of a landscape, topographic variables are often strongly correlated (Amatulli et al., 2018), and therefore suggest that topography is an important determinant of vegetation cover across spatial scales. A rugged landscape might help to conserve areas of native vegetation cover by limiting their accessibility, a phenomenon known as *de facto* conservation (Joppa et al., 2008). In addition, rugged areas likely have shallower soils, which could affect agricultural suitability. A more rugged landscape not only prevents land use change and deforestation, other studies suggest that it could also affect other biodiversity aspects, such as, extinction rates and the spread of introduced species (Duncan et al., 2013; Jardim and Menezes de Sequeira, 2008; Steadman, 1995; Steadman and Martin, 2003). Therefore, to ensure the conservation of island biodiversity and native habitats, regional conservation policies should prioritize biodiversity hotspots in accessible locations. Furthermore, because islands are leading loci of the global sixth mass extinction (Barnosky et al., 2011; Kier et al., 2009), they deserve strong international support while developing, implementing, and monitoring such conservation policies.

Human impacts and population density in the past

Several studies have used human population density to predict future global biodiversity changes (McKee et al., 2004) and suggest this density is an important factor in guiding global conservation efforts (Ceballos et al., 2017; Cincotta et al., 2000; Tilman et al., 2017), while other studies have cautioned about placing too much emphasis on population density as a driver of land cover change (Geist and Lambin, 2006; Lambin et al., 2001). On islands, the relationship between population density and native vegetation could be expected to be particularly strong, since they are clearly constrained by physical boundaries. However, we find that human densities on the 30 Eastern Atlantic Islands were a poor predictor of the amount of native vegetation remaining on those islands. One explanation for this discrepancy is that the link between human population density and biodiversity change at local and regional scales might be less straightforward than at the global scale as environmental impacts can be exported offshore.

In addition, much of the transformation of island ecosystems has already happened in the past when population density of an island and local resource use were arguably more closely

intertwined (Norder et al., 2017). On Hawaii, for example, rapid historical population growth was closely linked with agricultural intensification in the past (Kirch, 2007). Native vegetation cover on islands in the Eastern Atlantic might therefore better reflect past demographic fluctuations, rather than modern population density. For example, modern population density of the Canary Islands and Gulf of Guinea exceeds that of the Azores, while for most of the previous five centuries this pattern was the opposite. Similarly, differences between islands in terms of modern landscape modification might also deviate from past patterns. Because historical land use has strong legacies on present-day biodiversity patterns (Foster et al., 2003), for future studies it would be relevant to include historical land use data as well. However, while an existing spatially explicit database of historical land use (Klein Goldewijk et al., 2011) could allow for such analyses on a global scale, its resolution is currently too coarse for many islands. With the development of global databases at finer resolutions such analyses might become increasingly feasible. Another approach for future comparative studies like ours could be to include categorical variables that classify the history of an island. For example, regarding subsistence strategies (Rick et al., 2013), or in case an island was later colonized by Europeans, the type of colony that was established (Lightfoot et al., 2013). However, while such an approach could help discerning patterns across islands, it 'flattens' history; there seems to be a trade-off between historical depth and geographical generalizability. While mixed-method approaches that integrate qualitative written historical evidence with quantitative statistical approaches (Haldon et al., 2018), could enhance our understanding of human-environment interactions across spatial and temporal scales, such integration should not necessarily be achieved in a single study. Here, we compared islands in terms of modern socio-environmental variables and used historical reconstructions to contextualize statistical findings. Future studies could explore the extent to which historical socioeconomic developments match the timing of environmental changes stored in pollen diagrams or charcoal records (de Nascimento et al., 2009; Gosling et al., 2017; Nogué et al., 2017).

Local human-environment interactions in the anthropocene

The loss of native habitat is just one aspect of the ecological changes in the Eastern Atlantic Islands following human colonization. The islands have further been transformed due to the introduction of exotic species, extinction of natives and endemics, and abiotic changes, such as soil erosion (Table A.3). The Eastern Atlantic Islands are not unique in this regard, other islands worldwide have been transformed by human activities in similar ways (Boivin et al.,

2016; Braje et al., 2017; Graham et al., 2017; Rick et al., 2013). In the Eastern Atlantic Islands, the ecological outcomes of human activities appear to be strongly modified by the local environmental context, with island topography playing a major role. Similar findings have been reported for other island worldwide. In the Caribbean, for example, prehistoric people transformed island environments, but also adapted to them (Fitzpatrick and Keegan, 2007). In the Pacific, deforestation was found to be the outcome of environmental drivers as well as cultural responses shaped by environmental constraints (Atkinson et al., 2016). On many places around the world, including many islands, people have altered their local environment already hundreds to thousands of years ago (Stephens et al., 2019). Over the last centuries, these local scale changes have accumulated to drive planetary scale changes in the Earth system. The recognition that human activities have become key drivers of global change in ecosystems and environments has given rise to the concept of the "Anthropocene" (Crutzen and Stoermer, 2000; Steffen et al., 2007). Anthropocene narratives tend to present humanity as the single driving force of global change, with nature as a passive receiver, while neglecting the preceding local-and regional scale interactions between societies and environments (Braje, 2015; Braje and Erlandson, 2013b; Rick et al., 2013). In the Eastern Atlantic islands, for example, human impacts are shaped by and situated within environmental contexts. Although human impacts have become a major force in planetary change, the Anthropocene is not only the product of anthropogenic drivers, but is co-produced by many local societies and environments. While much emphasis has been placed on global modeling approaches and on the analysis of iconic cases, studies that compare human-environment interactions across different locations might be particularly suitable for exploring potential pathways towards sustainable futures in the Anthropocene.

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GENERAL CONCLUSIONS AND FUTURE PERSPECTIVES

FOCUS OF THE THESIS AND KEY QUESTIONS

The overarching aim of my thesis was to understand how environmental and societal conditions, and their interactions, shaped modern biodiversity patterns. In the first part of this thesis I have quantified geographical island dynamics over the Quaternary and analysed to what extent their imprint can still be observed in biodiversity patterns today. In the second part of this thesis I have made a reconstruction of environmental and societal trends in the past and explored legacy effects on present-day ecosystems. In this final part, I will provide an overview of the main findings of my thesis and discuss how changes over the last centuries and millennia relate to biogeographical dynamics over longer timescales. I present the conclusions that emerge from this thesis as a whole and outline potential avenues for future research to enhance our understanding of the relationship between anthropogenic- and environmental drivers of biodiversity.

MAIN FINDINGS OF THE THESIS

Island biodiversity legacies of Quaternary dynamics

Modern island characteristics are not representative for the long term. This is because islands have changed in response to geological and climatic processes, such as sea level fluctuations. Sea levels were relatively high during warm interglacial periods, and low during the cooler glacials. While it has long been hypothesized that such dynamics could have affected the distribution and evolution of island species (Mayr, 1944; Heaney, 1985), testing this relationship remained challenging because geographical changes of islands in response to sea level fluctuations had not been quantified. To fill this gap, I have built the first global spatially-explicit database on sea level driven changes in island configuration over the last glacial-interglacial cycle (section 1.1; Norder *et al.*, 2018). At times of lower sea levels, islands were larger and less isolated than today, and some islands fused with other islands. As a consequence of bathymetric (underwater topography) differences, each island responds uniquely to changes in global sea level (although other aspects also play a role, see Norder *et al.*, 2018). Consequently, two islands with a similar size today, might have had a very different area in the past, which must have had profound effects on species distributions. With the quantification of these dynamics

Main finding

Each island responds in a unique way to global sea level fluctuations, resulting from differences in topography (section 1.1; Norder *et al.*, 2018).

for a large number of islands it became possible to explore the role of past geography in shaping modern biodiversity patterns.

While we had already explored the role of past island geography at lower sea levels (Rijsdijk *et al.*, 2014; Simaiakis *et al.*, 2017), in those studies we focused on one static snapshot in time: the extreme low sea level ~21 kyr ago during the Last Glacial Maximum. These conditions are however highly exceptional: for only 2% of the time over the last ~800 kyr, sea levels were below this level. For most of the Quaternary, sea levels fluctuated between the extremes of the Last Glacial Maximum and interglacials like the Holocene. We therefore set out to explore to what extent modern biodiversity patterns reflect past conditions, not only short-lasting ones, but also those that were more representative of the Quaternary. Taking advantage of the Palaeo-Islands and Archipelago Configuration database (section 1.1; Norder *et al.*, 2018), for 53 islands we tested to what extent the current distributions of land snails and angiosperms reflect past conditions (section 1.2; Norder *et al.*, 2019). We found for both taxa that modern biodiversity patterns are imprinted by the geographical characteristics of islands in the past. More specifically, past conditions that were longer-lasting could better explain biodiversity patterns than exceptional conditions during the Last Glacial Maximum. This pattern was most evident for single-island endemics, species that have generally adapted to a particular island over evolutionary timescales. The insight that long-lasting geographic configurations prevailing during the Quaternary better explain modern single-island endemic distribution patterns than modern and LGM conditions is novel to science.

Main finding

The modern distribution of single-island endemics across taxa is imprinted by long-lasting Quaternary conditions (section 1.2; Norder *et al.*, 2019).

Biodiversity legacies of human-environment interactions

While islands are microcosms of global change, the drivers and consequences of biodiversity change in the Anthropocene manifest differently across scales. We explored whether the impacts of past human-environment interactions on islands could still be observed today. On the island Mauritius (Indian Ocean), past human activities in the four centuries following human colonization led to the near complete deforestation of the island and resulted in permanent biodiversity loss due to the extinction of many endemic species. Historic records of deforestation allowed for comparing the rate and magnitude of changes following human colonization to pre-human background rates. For Mauritius, we have analysed the relationship

between historical deforestation an soil loss (section 2.1; Norder *et al.*, 2017). Our analyses show that rates of soil loss largely exceed geological background rates, resulting in a cumulative soil loss since first human settlement that is five times higher compared to the amount of soil that would be lost under pre-human conditions (over the same amount of time). When rates of soil loss exceed soil formation rates, this results in a net decrease of the total soil stock in a region over time, a phenomenon which we termed 'soil debt' (Norder *et al.*, 2017). Because soils form the basis for ecosystem functioning, and for the provisioning of ecosystem services to society, a soil debt could undermine the sustainability of a social-ecological system. Although the consequences of soil loss for ecosystem services provisioning can be partly offset by imports from elsewhere (e.g. food, fuel, fertilizers), the native ecosystems are negatively affected and the self-sufficiency of insular societies is compromised. We also found that patterns of deforestation and soil loss varied over time: gently sloping coastal zones were impacted earlier than steeper slopes and higher elevations. Based on this finding for Mauritius I became curious to see whether topography also shaped human-environment interactions on other islands. Therefore, we started a comparative analysis of 30 islands in the Eastern Atlantic to find out why ecological outcomes of human-environment interactions differ across islands (section 2.2; Norder *et al.* in revision). We specifically focused on the extent of native vegetation cover because it provides a habitat for many native and endemic island species. To estimate the extent of native vegetation cover per island we combined information from land use land cover maps and databases. In a statistical framework, we analysed to what extent native vegetation cover could be explained by environmental and societal predictors. We discovered that societal predictors were less important than environmental variables in explaining the variance in native vegetation cover across islands and that island topography was by far the strongest predictor of differences in native vegetation cover. Our findings suggest that native

Main finding

The removal of native vegetation following human settlement on Mauritius caused soil loss rates to outpace geological rates of soil loss and formation, undermining the sustainability of ecosystems and society as a result (section 2.1; Norder *et al.*, 2017).

Main finding

Rugged islands have a larger proportion of native vegetation cover than smoother ones, the extent to which native ecosystems are transformed by human activities depends on island topography (section 2.2; Norder *et al.* in revision).

vegetation on rugged islands is better protected to land use changes. These findings also highlight that human impacts on island biodiversity are strongly modified by environmental conditions.

SYNTHESIS OF PART 1 AND 2

Island biogeography in the Anthropocene: outside the Quaternary range?

My results indicate that modern social-ecological systems on islands have their roots in the geological and historical past. So far, I have dealt separately with biogeographical dynamics over the Quaternary, and more recent human-environment interactions. In the following paragraphs I will explore how they are related. Over millions of years, climatic, geological, evolutionary and ecological processes interacted to shape island life, only over the last centuries to millennia, human activities were added to this mix. Therefore, modern biogeographical patterns on islands should be understood not only as being the outcome of geographical and biological processes, but anthropogenic processes as well (Figure 1; Helmus *et al.*, 2014).

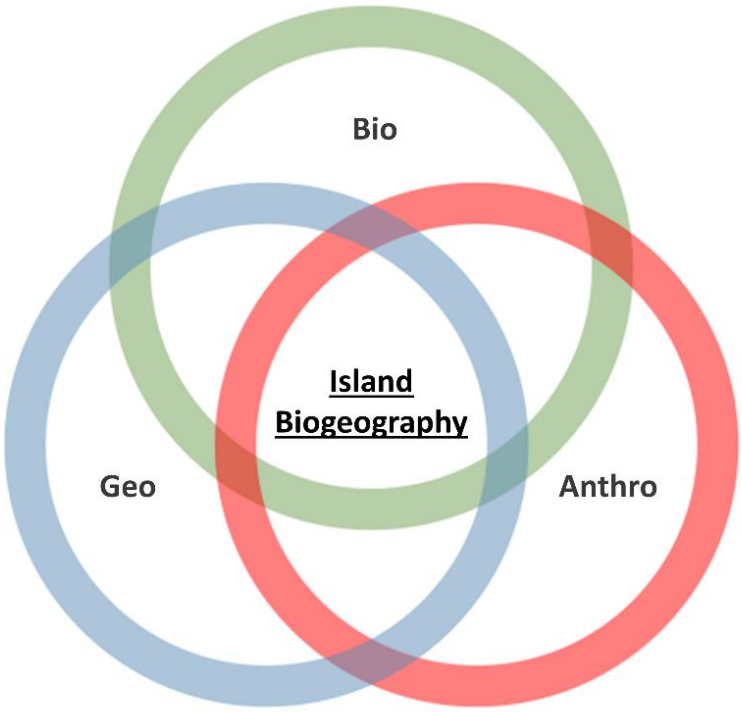

Figure 1. Venn-diagram illustrating the interdisciplinary character of island biogeography. In order to understand insular biodiversity patterns we need to integrate geographical, biological, and anthropogenic factors (figure modified from Norder & Rijsdijk, 2016).

The Equilibrium Model of Island Biogeography (MacArthur & Wilson, 1963, 1967) proposes that species richness on islands is an equilibrium resulting from the rate of extinction, and the rate of immigration. In turn, these rates are defined by the abiotic island characteristics area and island isolation. However, as became apparent from the first part of this thesis, island characteristics are highly dynamic over the Quaternary. With rising sea levels, low-lying parts of islands submerged, resulting in the flooding of native habitats near the coast. Compared to most of the Quaternary, islands – and consequently, the extent of their native habitats – are exceptionally small and fragmented under today's interglacial conditions. On top of this, the area of native habitat has been further reduced through land use/land cover change following the colonization of islands by humans over the last centuries and millennia. Area loss resulting from sea level rise, and area loss resulting from land use change might not be directly comparable. For example, land uses (such as agricultural fields) surrounding patches of native vegetation could still provide transient habitat for native terrestrial species, in contrast to land lost by sea level rise on true islands (Ricketts, 2001; Kupfer *et al.*, 2006). Nonetheless, for a comparison of human-driven habitat loss to pre-human baselines, sea level driven changes in island area might provide a suitable analogy. Such a comparison could provide a first indication of the differences in rates and magnitude resulting from both environmental and anthropogenic drivers of native habitat loss (Figure 2). Following the arrival of humans, the total extent of native habitat, that was already in a contracted interglacial state, was further reduced due to land use/land cover change. Despite operating on vastly different timescales, both the impact of sea level fluctuations and land use change on native habitat was strongly influenced by island topography. However, the rate at which the area of native vegetation was reduced following human colonization appears to be much larger compared to baseline dynamics (Figure 2). On Mauritius for example (Figure 2c), the sea level driven area reduction that took place since the Last Glacial Maximum is drastically outpaced by the rapid transformation of native habitat in only four centuries of human settlement. The outcome begs the question whether native natural systems that adapted to natural reductions in habitats by sea level change, can keep up with the much higher rates and magnitudes of reductions induced by humans.

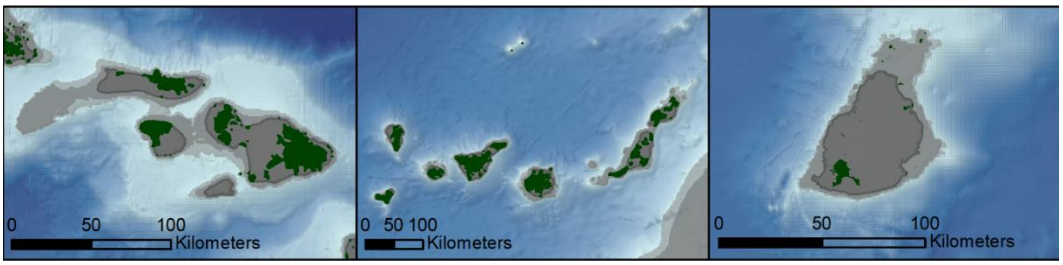

Figure 2. Change in habitat area resulting from land use conversions and sea level fluctuations for a) the Hawaiian Islands (Molokai, Lanai, Maui, and Kahoolawe), b) the Canary Islands, and c) Mauritius. The grey areas indicate the extent of islands at three sea level stands: at high present-day interglacial sea level where islands are exceptionally small, at intermediate sea level (calculated as the median over the last 1 million years; section 2.3; Norder et al., 2019), and at the extreme low sea level of the Last Glacial Maximum (Data obtained from Norder et al., 2018; see also section 2.2. The green areas indicate the outline of areas with some kind of legal protection. Data on natural reserves for Hawaii were obtained from the State of Hawaii – Office of Planning (https://planning.hawaii.gov/gis/download-gis-data/). For the Canary Islands, I show all protected areas which are part of the "Red Canaria de Espacios Naturales Protegidos" (data obtained from https://visor.grafcan.es). For Mauritius, I used the outline of all areas that are part of the 'Existing Protected Area Network' (Republic of Mauritius, 2017).

In the preceding paragraph, I have explored how the area of islands and their native habitats change resulting from sea level oscillations and land use conversion. Besides island area, isolation is another island characteristic that drives biogeographical processes. How has island isolation changed over the Quaternary, and how does this differ from human-induced changes? The change in isolation resulting from Quaternary sea level fluctuations, measured as distance between islands as well as between islands and continents, is negligible for oceanic islands (section 1.1; Norder *et al.*, 2018). The merging of islands at lower sea levels, such as the Maui Nui complex in Hawaii and Mahan in the Canary Islands (Figure 2a,b), occurred rarely within oceanic archipelagos (section 1.1; Norder *et al.*, 2018). These modest changes in island isolation over the Quaternary contrast with the increased socioeconomic connectivity when islands were first settled by humans. For example, Mauritius (section 2.1; Norder *et al.*, 2017) and the Atlantic Ocean Islands (section 2.2; Norder *et al.* in revision) became nodes in emerging global trade networks. Consequently, while the ocean formed a geographical barrier throughout the Quaternary, and many millions of years before that, over a few centuries it has been replaced by a hyper-connected web encompassing many islands globally. As such, the current degree of connectivity is unprecedented in the Quaternary. In the general introduction of this thesis I included an image of Pangea, the supercontinent that existed 225 Myr ago when all continents were joined in a single land mass. The term 'New

Pangea' (Rosenzweig, 2001) has been coined to highlight that previously distant locations have become reconnected. However, this analogy might also be appropriate in highlighting just how exceptional the current conditions are compared to deep-time dynamics.

FUTURE LINES OF RESEARCH

I really enjoyed the last four years working on this thesis and I think my findings have contributed to a better understanding of how human-environment interactions on islands relate to long-term biogeographical dynamics. However, the insights developed in this thesis also revealed some methodological and theoretical research gaps. In this last section I will briefly outline these gaps and suggest some potential avenues for future research to address them.

Geographical island dynamics and modern biodiversity legacies

In section 1.1 (Norder *et al.*, 2018), we quantified changes in island geography and archipelago configuration in response to global sea-level fluctuations. However, there are several other processes that affect island geographical dynamics, such as volcanism, erosion, and regional variations in sea level. Currently it is unknown to what extent these different processes contribute to changes in island geography. An important avenue for future research will therefore be to quantify the relative contribution of each of these variables to island geography. However, while this has been done for individual islands and archipelagos (Ali & Aitchison, 2014), it will be challenging to develop detailed reconstructions for islands across multiple archipelagos. Therefore, to understand how biodiversity patterns across islands have been shaped by different processes in the past, it will be helpful to develop models that incorporate sea level fluctuations and geological dynamics. A possible approach could be to integrate our recently developed Glacial-Sensitive Model (Fernández-Palacios *et al.*, 2016) with the General Dynamic Model for the ontogeny of volcanic oceanic islands (Whittaker *et al.*, 2008; Borregaard *et al.*, 2017). The challenge here will be to develop models that are both general, but also flexible enough to incorporate differences between island types (Ali, 2017), geological dynamics at the scale of the archipelago, and regional variations in sea level.

Question for future research

What is the relative contribution of sea level fluctuations and geological dynamics to changes in island geography?

Our analysis of the role of sea-level fluctuations in shaping island biodiversity patterns (section 1.2; Norder *et al.*, 2019) shows that it is worthwhile to compare archipelago configurations at alternative global sea level stands. Although it is encouraging to find that one global sea level affected single-island endemism richness across islands, within individual archipelagos there might be specific sea level thresholds at which islands become connected or separated (or where island area rapidly increases). Earlier studies have generally asked the binary question of whether islands were connected during the Last Glacial Maximum or not. I think it is more interesting to ask at which sea level threshold, how often, and for how long, islands merged or separated. Therefore, I hope to explore in the near future to what extent archipelago-specific sea level thresholds show imprints on modern species distributions. With such a change in perspective we could revisit earlier studies and explore how island connectivity affects beta diversity (Rijsdijk *et al.*, 2014), or how the splitting and merging of populations by rising and falling sea level affects diversification (Heaney *et al.*, 2005; Papadopoulou & Knowles, 2017).

Question for future research

How has the repeated merging and splitting of islands at archipelago-specific thresholds affected biodiversity patterns?

Human-environment interactions in the Anthropocene

In section 2.1 (Norder *et al.*, 2017), we modelled the relation between deforestation and soil loss over time, and compared the rates following human settlement to pre-human rates. This approach is relatively uncommon; studies that analyse past human-environment interactions often do not make a comparison to pre-human changes. There are exceptions off course, such as some paleo ecological studies (e.g. Willis & Birks, 2006; Nogué *et al.*, 2017) and studies comparing extinction rates over time (Barnosky *et al.*, 2011). For future research I think it will be worthwhile to explore novel ways in which human-induced changes could be compared to pre-human dynamics. Comparing rates of habitat loss resulting from land use change to the maximum area loss due to Quaternary sea-level fluctuations could be a possible way of doing that. Islands will be ideal model systems for such comparisons because of their relatively recent and well-defined timing of human settlement. Building comprehensive reconstructions of past human-environment interactions, and comparing them

Question for future research

How have human-environment interactions evolved over time and how do they differ from pre-human dynamics?

to pre-human dynamics, will involve the integration of insights from different sources and disciplines. Nonetheless, such integration should not necessarily be achieved in the same study, but could be reached by combining insights from different studies in the same region. For example, after finishing our study of Mauritius presented in section 2.1 (Norder *et al.*, 2017), we did a follow-up analysis of charcoal records and data on species extinction and introduction on the same island (Gosling *et al.*, 2017).

In section 2.2 (Norder *et al.* in revision) we have analysed the relative contribution of societal and environmental factors in shaping modern ecosystem outcomes across 30 islands in the Atlantic Ocean. We adopted an interdisciplinary approach because we observed that earlier studies rarely did an integrated analysis of societal and environmental variables. While our study is a step towards understanding their relative importance, our findings also underscore the challenges of integrating qualitative historical information and modern quantitative variables. In section 2.2 (Norder *et al.* in revision) we have suggested ways in which past societal trends could be incorporated in statistical analyses; this would allow for a global analysis of the relative contribution of contrasting societal histories and geographic island characteristics. However, this is one quantitative approach to a broader research challenge, namely interdisciplinary integration. On a more general note, for future studies on human-environment interactions it will be crucial to complement methods from different scientific domains, and perhaps more importantly, find out how and why their answers differ. A possible way to assess this is by doing a cross-disciplinary literature review of published studies which have explored the contribution of anthropogenic and environmental drivers to shaping modern socio-ecological systems or, more specifically, a particular aspect of biodiversity (e.g. the number of species introductions or land cover change).

Question for future research

How have contrasting historical societal trends and geographical island characteristics shaped modern socio-ecological systems on islands globally?

Placing human-environment interactions in the context of deep-time

On every island where people arrived they encountered a unique world that had been shaped by environmental and biological processes over thousands to millions of years (Figure 3). Islands remind us that people are not actors on a static stage, but rather participants in a play that started long ago. Nonetheless, in a blink of geologic time, people managed to become a major driver in shaping island ecosystems and landscapes. While this is true for many islands

worldwide, there also exist large differences between islands in the way human-environment interactions have evolved over time. For future studies, I think it will be particularly fruitful to explore the range of variability across regions and how it has been shaped by contrasting environmental and societal conditions in the recent and distant past. Such an endeavour will require the integration of a wide range of sources and new collaborations across disciplines.

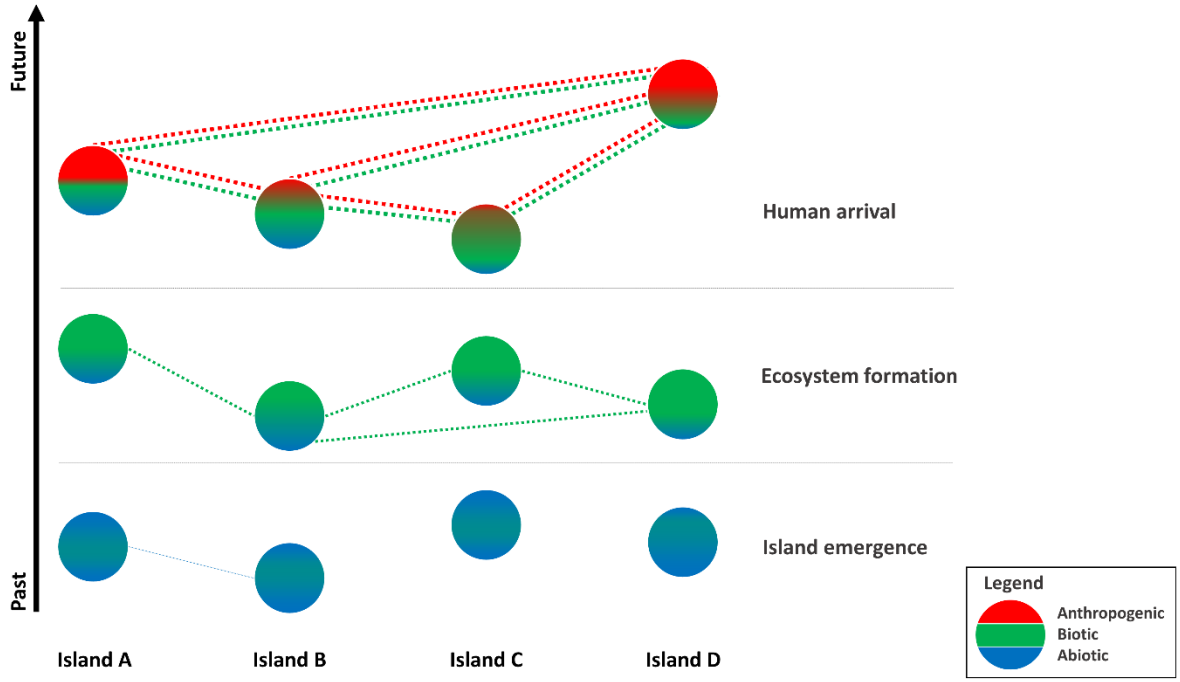

Figure 3. Island dynamics over the Quaternary and Anthropocene: each island is characterized by a unique interplay between abiotic, biotic, and anthropogenic factors. The onset of each of these factors differs between islands. In addition, the degree to which islands are connected to each other in terms of biological and sociocultural exchanges has increased over time (line thickness).

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APPENDICES AND SUPPORTING INFORMATION

Appendices corresponding to section 1.1

A global spatially explicit database of changes in island palaeo-area and archipelago configuration during the late quaternary

OVERVIEW OF APPENDICES

On the following pages you will find three appendices:

- Appendix S1, see also: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fgeb.12715&file=geb12715-sup-0001-suppinfo1.DOCX
- Appendix S2, see also: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fgeb.12715&file=geb12715-sup-0002-suppinfo2.DOCX
- Appendix S3, see also: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fgeb.12715&file=geb12715-sup-0003-suppinfo3.DOCX

LINKS TO ONLINE SUPPORTING INFORMATION

The PIAC database and the R scripts are shared at ISLANDLAB (http://islandlab.uac.pt/software/ver.php?id=28) and PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.880585), under the CC BY 4.0 license (https://creativecommons.org/licenses/by/4.0/).

APPENDIX S1

Percentage of time sea level was below certain level during last 1 Ma

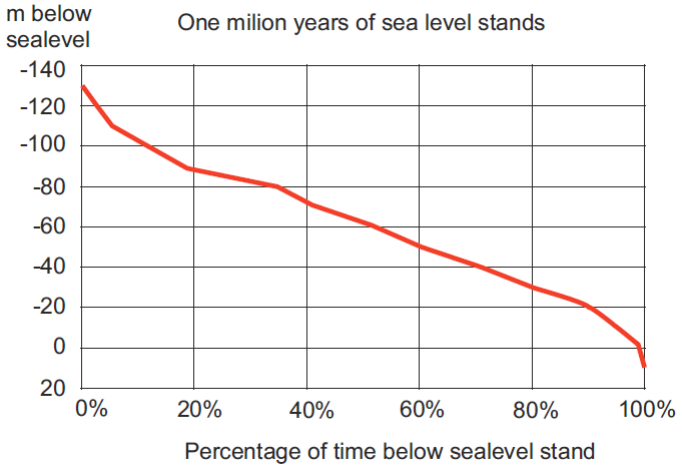

Figure S1. The percentage of time that the sea level was below a certain sea level during the last 1Ma (figure is based on data from Bintanja et al. (2005). 0 meters refers to the present sea level.

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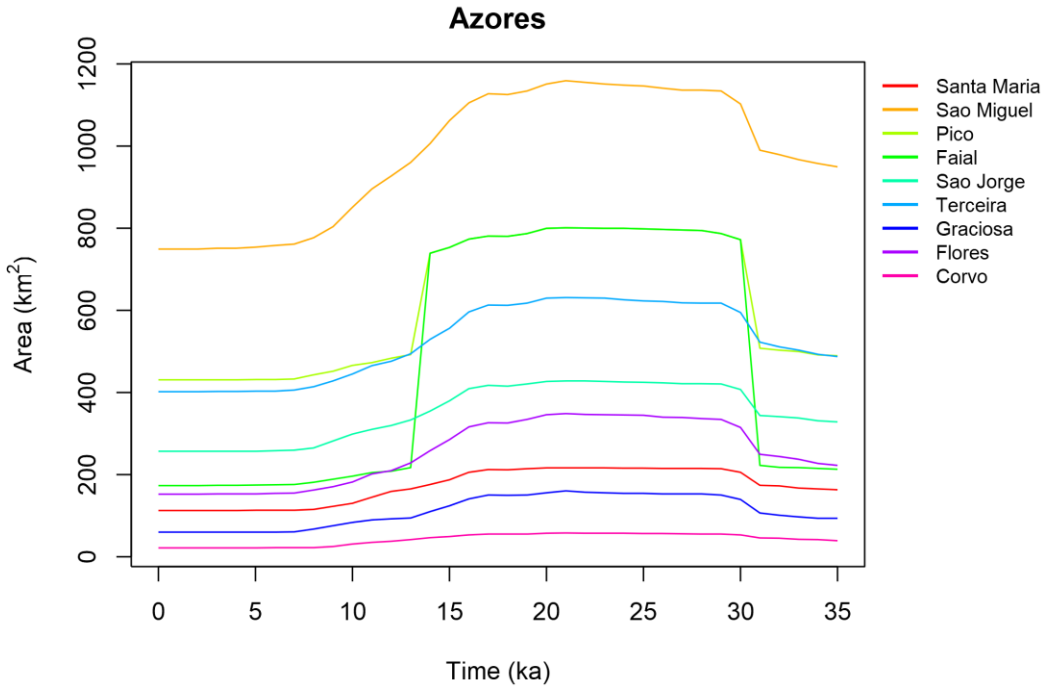
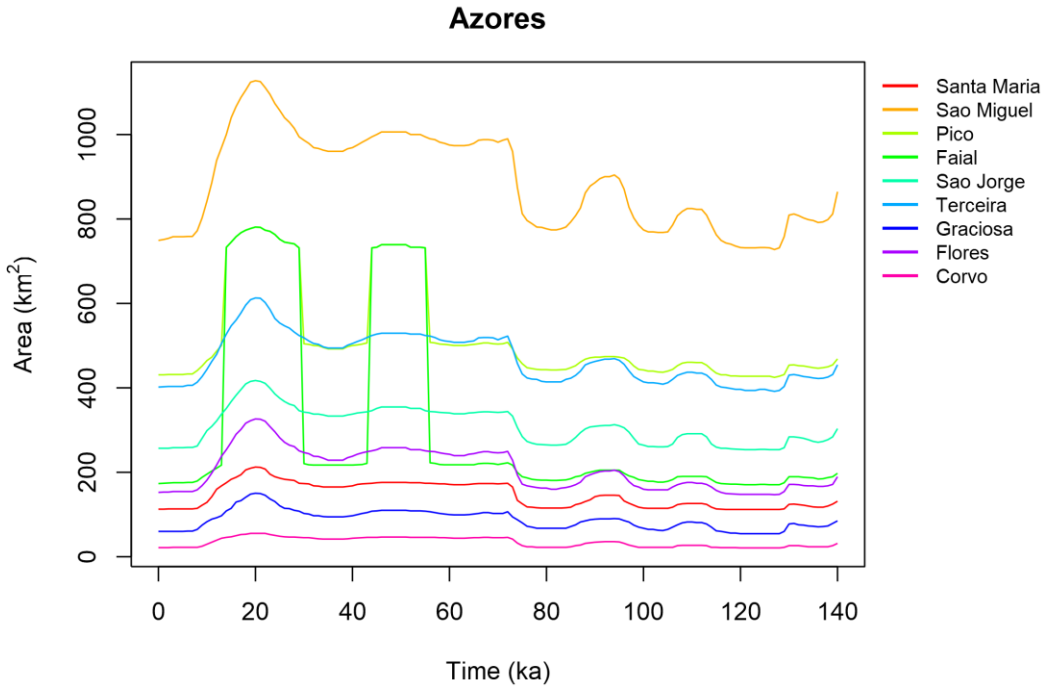
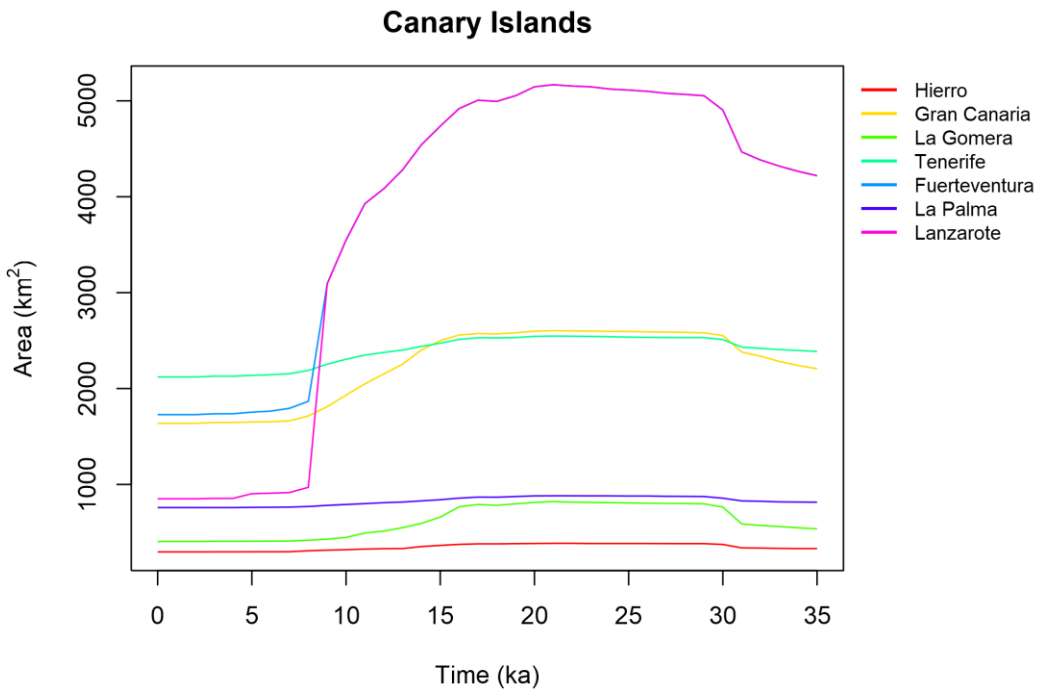
APPENDIX S2

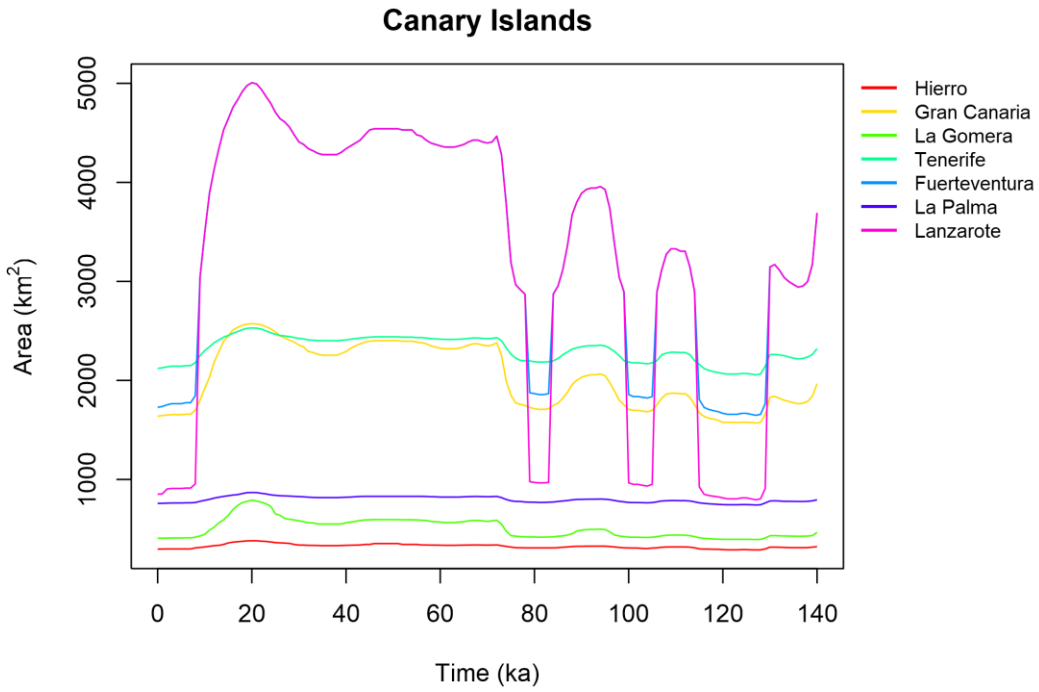
Paleo-area change (35ka and 140ka)

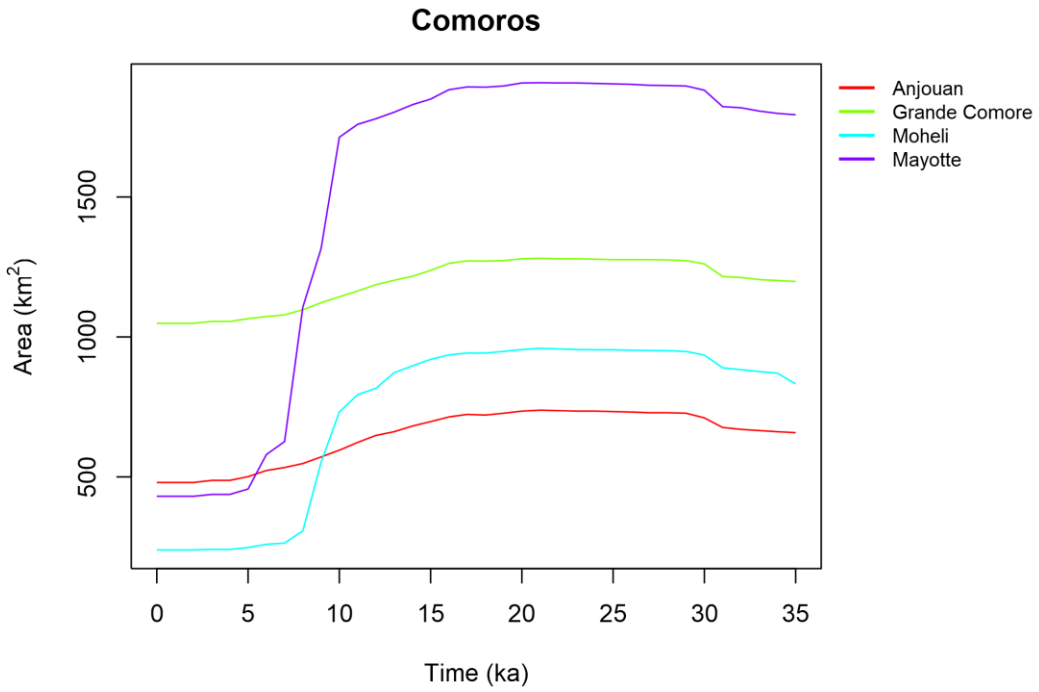
Changes in paleo-area over a period of 35ka and 140ka for a selection of seven archipelagos. The graphs were created by using respectively the sea level curve from Lambeck *et al.* (2014) and Cutler *et al.* (2003). The X-axis represents the time in ka before present; the Y-axis reflects the area of each island in km^2.

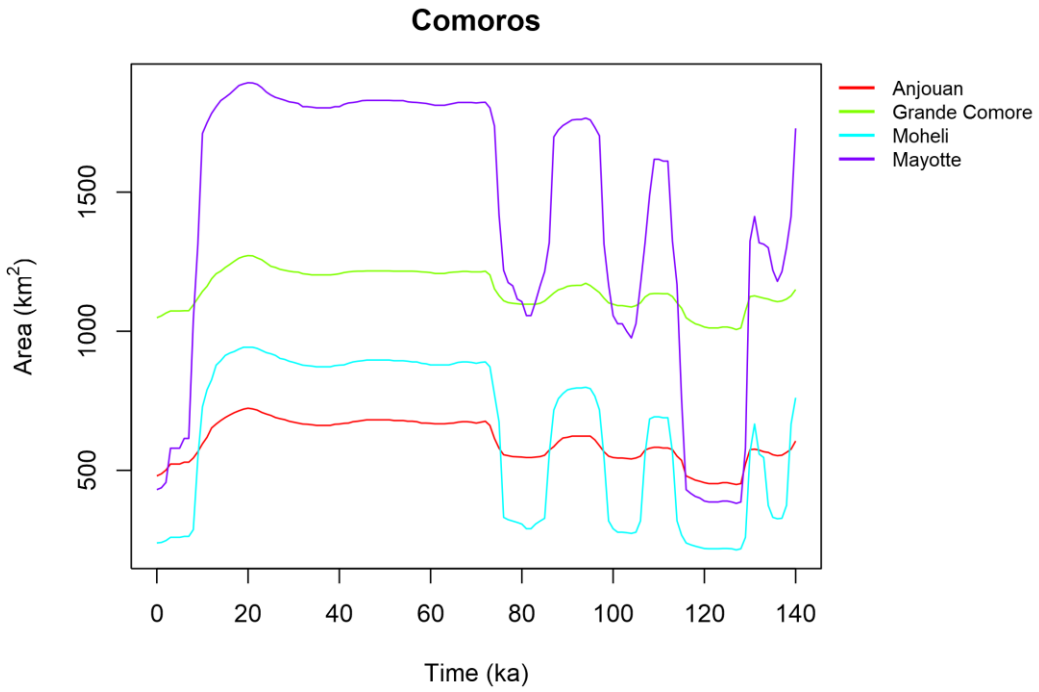

Azores
Area (km^2)
0
200
400
600
800
1000
1200
0
5
10
15
20
25
30
35
Time (ka)
Santa Maria
Sao Miguel
Pico
Faial
Sao Jorge
Terceira
Graciosa
Flores
Corvo

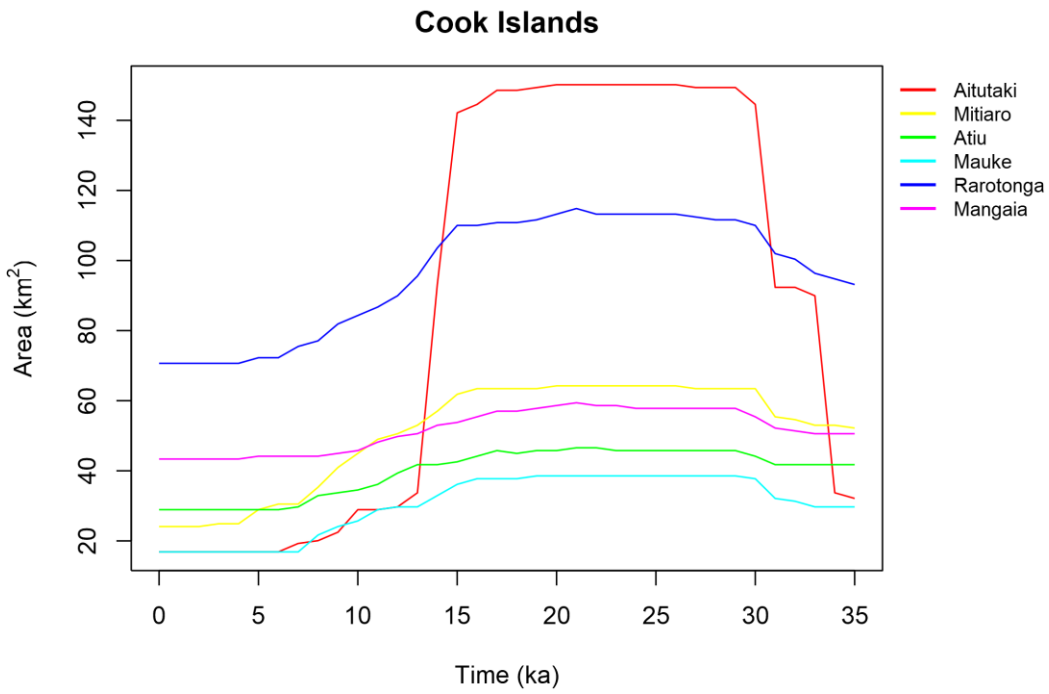

Azores
Area (km^2)
0
200
400
600
800
1000
0
20
40
60
80
100
120
140
Time (ka)
Santa Maria
Sao Miguel
Pico
Faial
Sao Jorge
Terceira
Graciosa
Flores
Corvo

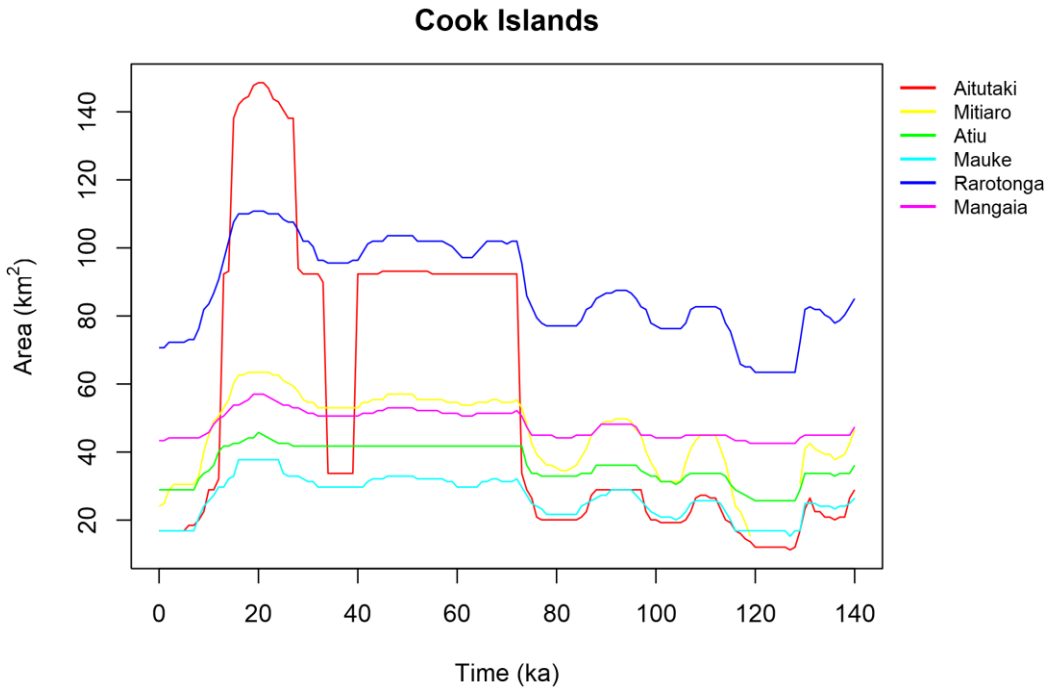

Canary Islands
Area (km^2)
1000
2000
3000
4000
5000
0
5
10
15
20
25
30
35
Time (ka)
Hierro
Gran Canaria
La Gomera
Tenerife
Fuerteventura
La Palma
Lanzarote

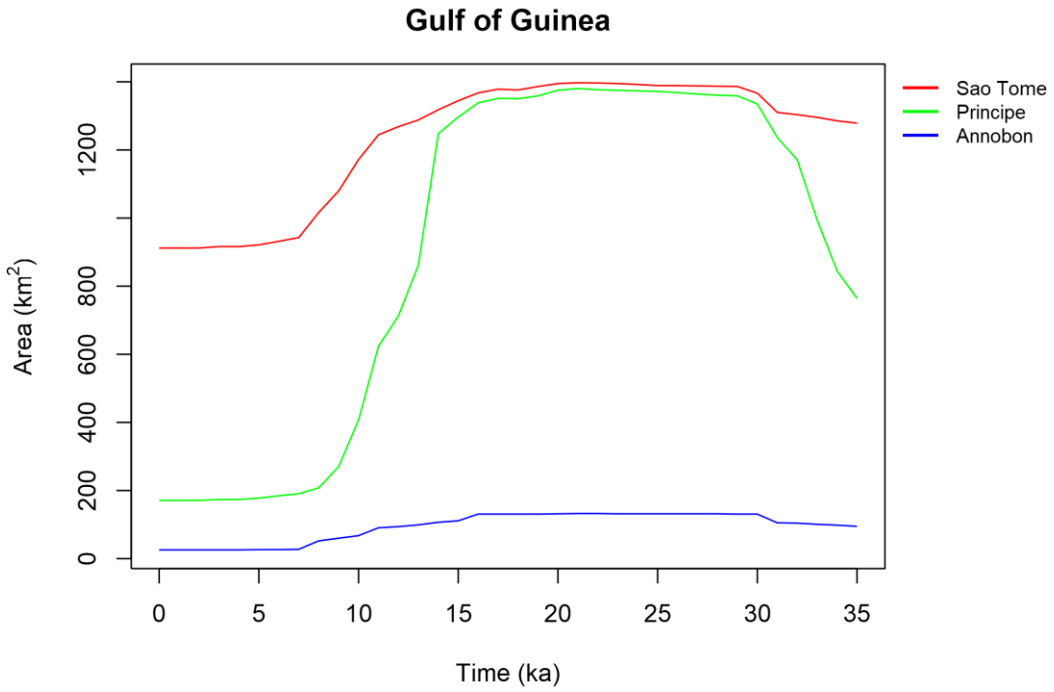

Canary Islands
Area (km^2)
1000
2000
3000
4000
5000
0
20
40
60
80
100
120
140
Time (ka)
Hierro
Gran Canaria
La Gomera
Tenerife
Fuerteventura
La Palma
Lanzarote

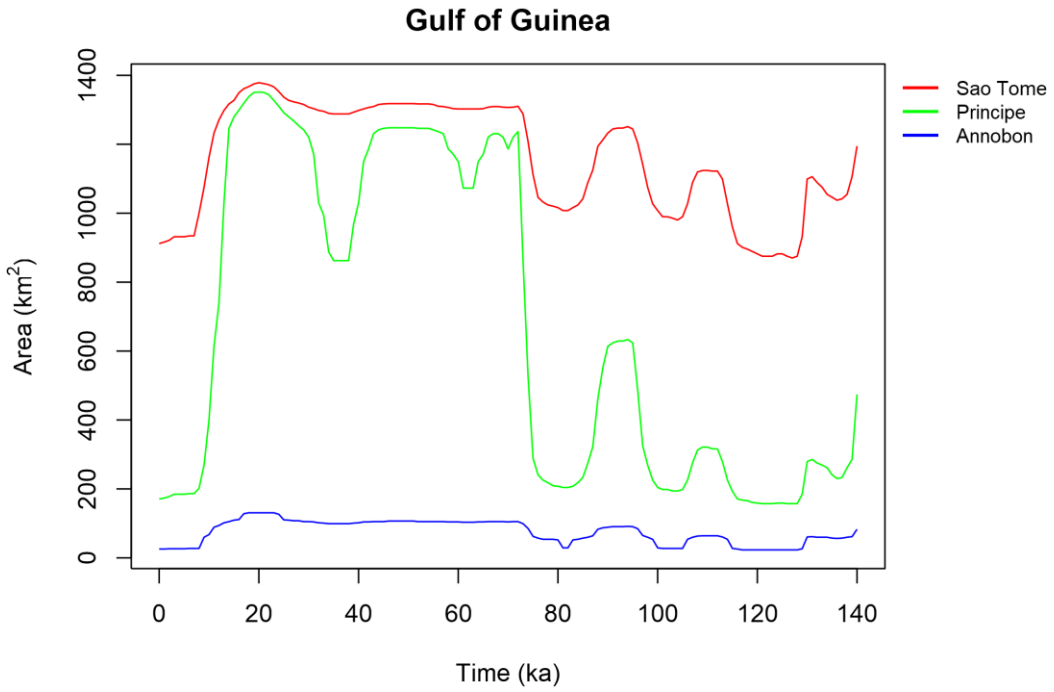

Comoros
Area (km^2)
500
1000
1500
0
5
10
15
20
25
30
35
Time (ka)
Anjouan
Grande Comore
Moheli
Mayotte

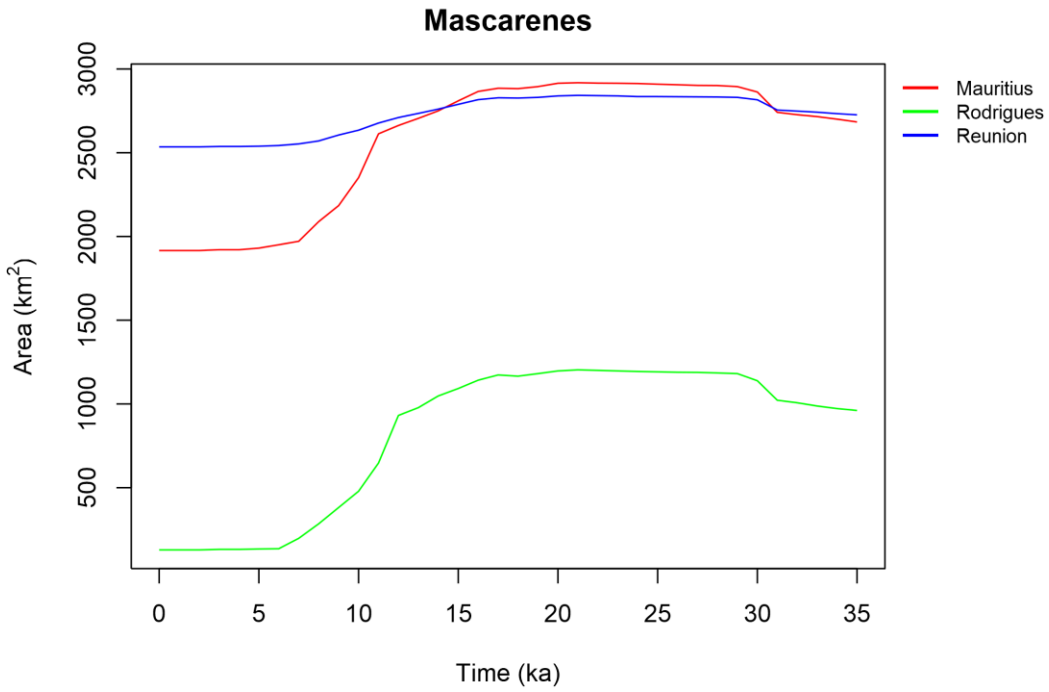

Comoros
Area (km^2)
500
1000
1500
0
20
40
60
80
100
120
140
Time (ka)
Anjouan
Grande Comore
Moheli
Mayotte

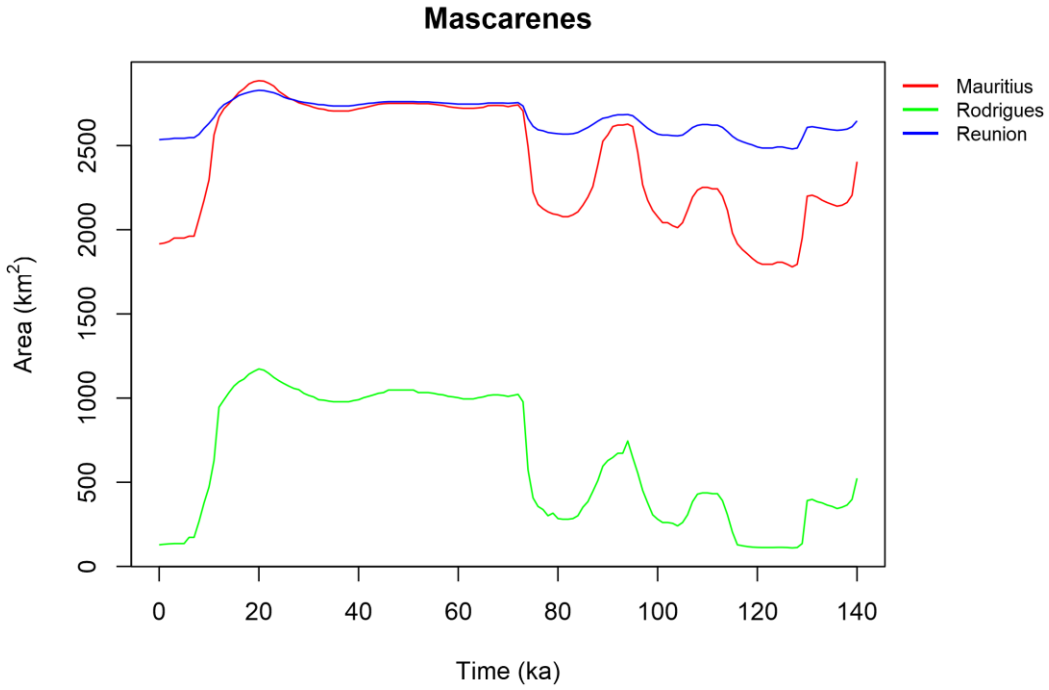

Cook Islands
Area (km^2)
20
40
60
80
100
120
140
0
5
10
15
20
25
30
35
Time (ka)
Aitutaki
Mitiaro
Atiu
Mauke
Rarotonga
Mangaia

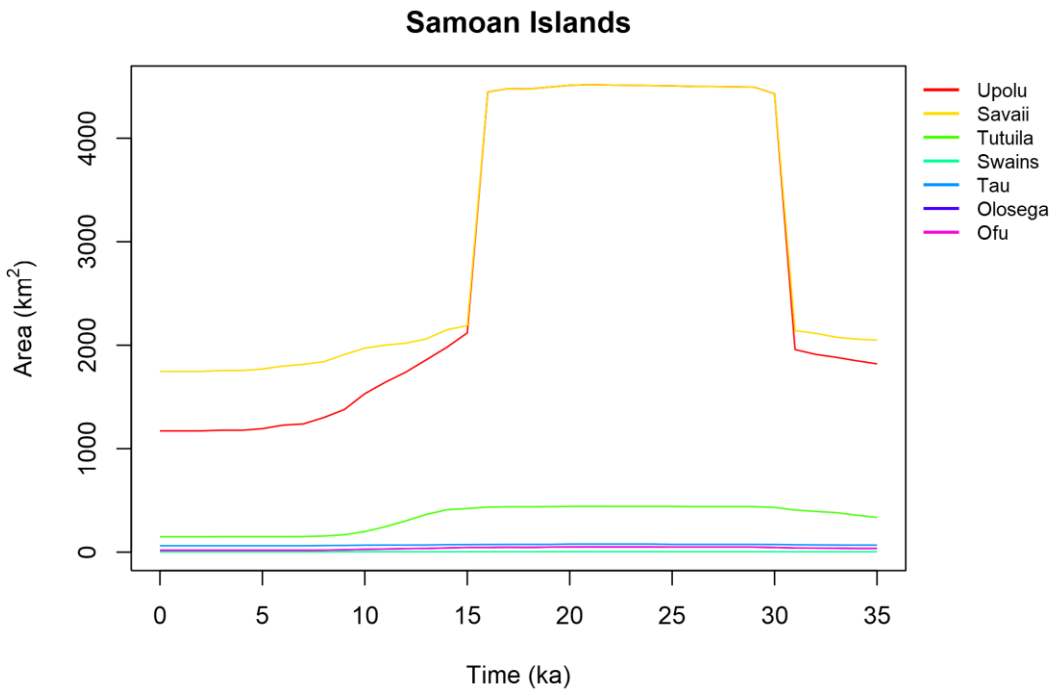

Cook Islands
Area (km^2)
20
40
60
80
100
120
140
0
20
40
60
80
100
120
140
Time (ka)
Aitutaki
Mitiaro
Atiu
Mauke
Rarotonga
Mangaia

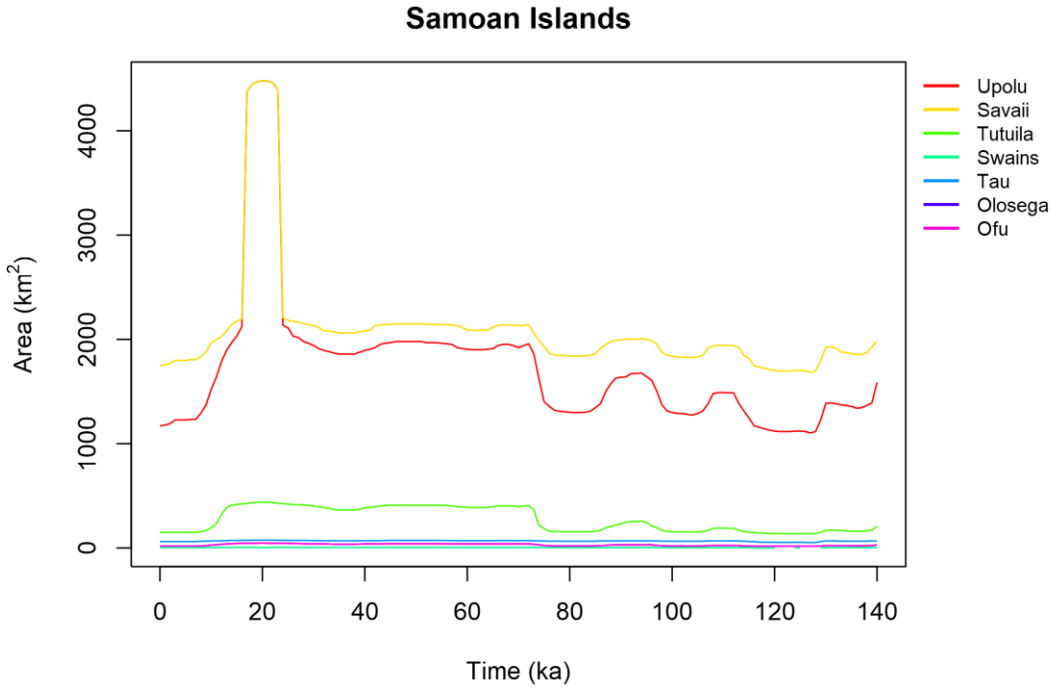

Gulf of Guinea
Area (km^2)
0
200
400
600
800
1200
0
5
10
15
20
25
30
35
Time (ka)
Sao Tome
Principe
Annobon


Gulf of Guinea
Area (km^2)
0
200
400
600
800
1000
1400
0
20
40
60
80
100
120
140
Time (ka)
Sao Tome
Principe
Annobon


Mascarenes
Area (km^2)
500
1000
1500
2000
2500
3000
0
5
10
15
20
25
30
35
Time (ka)
Mauritius
Rodrigues
Reunion


Mascarenes
Area (km^2)
0
500
1000
1500
2000
2500
0
20
40
60
80
100
120
140
Time (ka)
Mauritius
Rodrigues
Reunion


Samoan Islands
Area (km^2)
0
1000
2000
3000
4000
0
5
10
15
20
25
30
35
Time (ka)
Upolu
Savaii
Tutuila
Swains
Tau
Olosega
Ofu


Samoan Islands
Area (km^2)
0
1000
2000
3000
4000
0
20
40
60
80
100
120
140
Time (ka)
Upolu
Savaii
Tutuila
Swains
Tau
Olosega
Ofu

References

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APPENDIX S3

Accuracy and validation

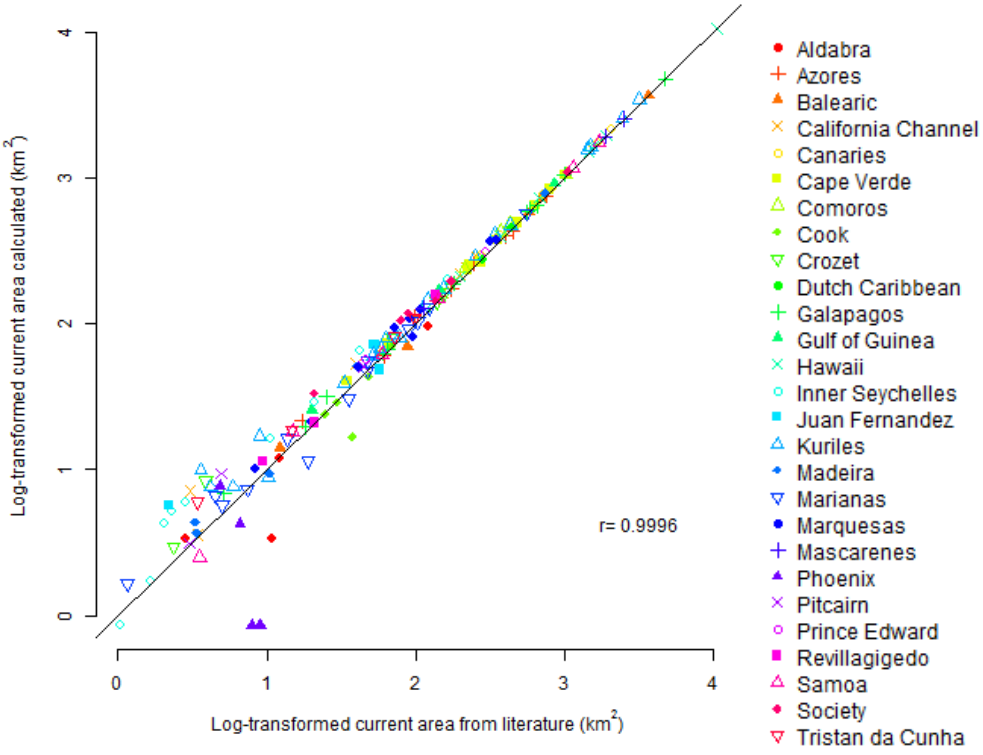

Figure S1. Relationship between current island area as calculated from the bathymetry Digital Elevation Model (DEM) by using the present-day sea level (0ka) and current area from www.gadm.org as reported in Weigelt et al. (2013).

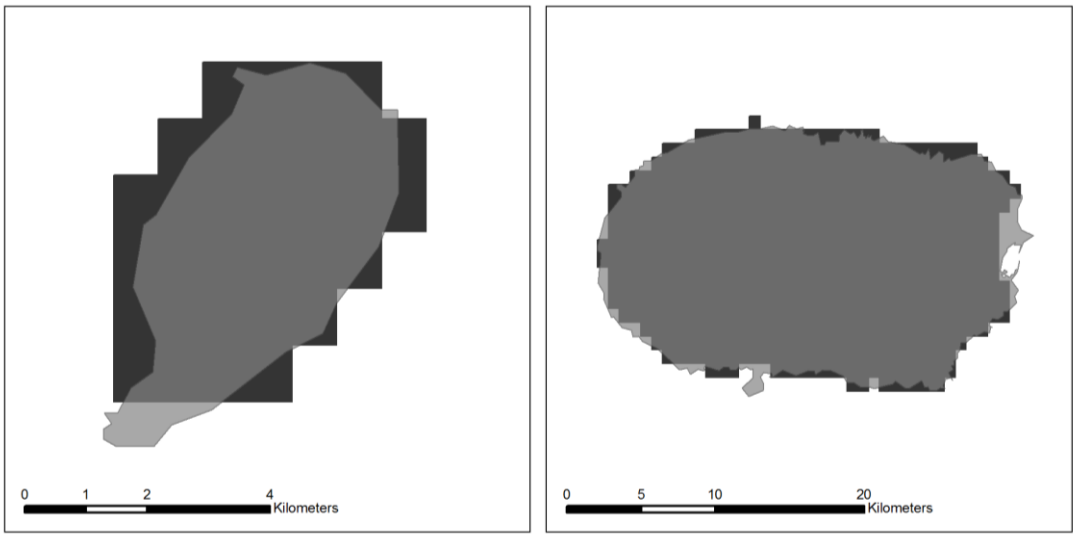

Figure S2. The proportional difference between calculated and reported area is larger for small islands (left) than for large islands (right). The area calculated from the bathymetry Digital Elevation Model (DEM) by using the present-day (0ka) sea level (dark grey grid cells) and reported area (light grey, semi-opaque polygons). Shown are two examples from the Azores (left: Corvo, right: Terceira).

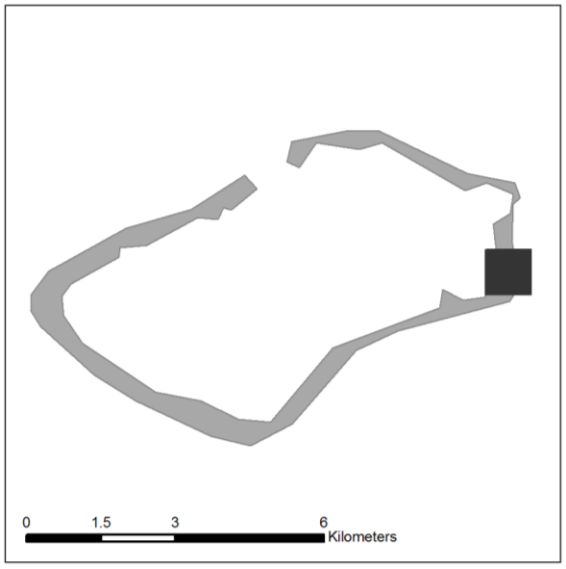

Figure S3. Orona (Phoenix archipelago), a low-lying atoll for which area is highly underestimated. The atoll is just a few meters above sea level (light grey, semi-opaque polygons). At the 30 arc-second resolution of the bathymetry Digital Elevation Model (DEM), only a single grid cell is above sea level (dark grey grid cells).

References

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Appendices corresponding to section 1.2

Beyond the last glacial maximum: island endemism is best explained by long-lasting archipelago configurations

OVERVIEW OF APPENDICES

On the following pages you will find one appendix:

- Appendix S1, see also: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Fgeb.12835&file=geb12835-sup-0001-Supinfo.docx

LINKS TO ONLINE SUPPORTING INFORMATION

The data supporting the results are archived in ISLANDLAB (https://islandlab.uac.pt/software/ver.php?id=32) and PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.893265) under the CC BY 4.0 license (https://creativecommons.org/licenses/by/4.0/).

APPENDIX S1

Table S1. Data sources for land snail data.

Archipelago	Sources
Azores	Martins (2011), updated with unpublished data of A.M.F. Martins, R.A.D. Cameron and B.M. Pokryszko
Canary Islands	Núñez & Núñez (2010), updated by Vega-Luz & Vega-Luz (2008), Holyoak & Holyoak (2009), Neiber *et al*. (2011) and unpublished data of M.R. Alonso and M. Ibáñez
Cook Islands	McCormack (2007)
Galápagos Islands	Dall & Ochsner (1928), Smith (1966), Coppois (1985), Parent & Crespi (2006) and references therein, Miquel & Herrera (2014), Parent *et al*. (2014)
Gulf of Guinea	Angus (1994)
Hawaiian Islands	Cowie *et al*. (1995) and Cowie (1995), updated by reference to Pokryszko (1997) for *Lyropupa*
Madeira	Seddon (2008) with some corrections and minor modifications (following Goodfriend *et al*., 1996; Cameron *et al*., 2007)
Mascarenes	Griffiths & Florens (2006)
Pitcairn	Preece (1995) and Preece (1998)
Revillagigedo	Thompson (2011)
Samoan Islands	Cowie (1998) with additional records from Cowie (2001) and Cowie *et al*. (2002).
Tristan da Cunha	Holdgate (1965), Preece & Gittenberger (2003), Gittenberger *et al*. (2006)

Table S2. Pearson correlation matrix for land snails for the following chorotypes: indigenous non-exotic (S_S), native non-endemic (N_S), endemic to single archipelagos (END_S), multiple island endemics (MIE_S), single island endemics (SIE_S). Total indigenous land snail richness (S_S) is dominated by endemic species. For our dataset of volcanic oceanic islands, the correlations between single island endemics and palaeo-island endemics were almost 100%. All correlations are significant at $P < 0.001$.

	S_S	N_S	END_S	MIE_S	SIE_S	PIE_{MED}	PIE_{FREQ}	PIE_{MIN122}	PIE_{GM}
S_S	1.000								
N_S	0.101	1.000							
END_S	0.983	-0.083	1.000						
MIE_S	0.816	-0.060	0.829	1.000					
SIE_S	0.973	-0.085	0.990	0.741	1.000				
PIE_{MED}	0.972	-0.090	0.990	0.744	0.999	1.000			
PIE_{FREQ}	0.973	-0.094	0.992	0.759	0.998	0.999	1.000		
PIE_{MIN122}	0.974	-0.092	0.993	0.761	0.998	0.999	1.000	1.000	
PIE_{GM}	0.974	-0.094	0.993	0.764	0.997	0.998	0.999	0.999	1.000

Table S3. Pearson correlation matrix for angiosperms for the following chorotypes: indigenous species (S_P), native non-endemics (N_P), single island endemics (SIE_P), palaeo-island natives (PN_P), and palaeo–island endemics (PIE_P). Total indigenous angiosperm richness (S_P) is dominated by native (non-endemic) species. For our dataset of volcanic oceanic islands, the correlations between single island endemics and palaeo–island endemics, and between natives and palaeo-natives was almost 100%. All correlations are significant at $P < 0.001$.

	S_P	N_P	SIE_P	PN_P	PIE_P
S_P	1.000				
N_P	0.982	1.000			
SIE_P	0.728	0.583	1.000		
PN_P	0.982	0.999	0.587	1.000	
PIE_P	0.746	0.608	0.988	0.605	1.000

Table S4. Island ages (Myr) and data sources per archipelago. Where possible we used the subaerial age of the oldest geological formation on the island. When there was disagreement between sources we generally used the most recent source.

Island	Age (Myr)	Archipelago	Sources
Corvo	0.7	Azores	Azevedo & Portugal Ferreira (2006), Calvert *et al*. (2006), Hildenbrand *et al*. (2014), Larrea *et al*. (2014), Sibrant *et al*. (2014, 2015a, 2015b), Ávila *et al*. (2016), Ramalho *et al*. (2017)
Faial	0.85		
Flores	2.16		
Graciosa	1.057		
Pico	0.27		
Santa Maria	5.7		
São Jorge	1.3		
São Miguel	0.88		
Terceira	0.39		
Fuerteventura	23	Canary Islands	Staudigel *et al*. (1986), van den Bogaard (2013)
Gran Canaria	15		
El Hierro	1.1		
La Gomera	11		
La Palma	1.7		
Lanzarote	15		
Tenerife	12		
Atiu	10	Cook Islands	Turner & Jarrard (1982), Clouard & Bonneville (2005)
Mangaia	21.9		
Mauke	6.3		
Mitiaro	12.3		
Rarotonga	3.6		
Española	3.5	Galápagos Islands	Poulakakis *et al*. (2012)
Fernandina	0.07		
Floreana	2.3		
Isabela	0.8		
Pinzón	1.7		
San Cristóbal	4		
Santa Cruz	2.3		
Santiago	1.4		
Príncipe	31	Gulf of Guinea	Dunlop & Fitton (1979), Lee *et al.* (1994)
São Tomé	15.7		
Hawaii	0.6	Hawaiian Islands	Ziegler (2002)
Kauai	5.25		
Lanai	1.6		
Maui	1.75		
Molokai	2.1		
Oahu	4		
Madeira	7	Madeira	Ramalho *et al*. (2015), Ávila *et al.* (2016)
Porto Santo	19		
Mauritius	8.9	Mascarenes	

La Réunion	2.1		McDougall (1971), Duncan & Hargraves (1990), Thébaud *et al*. (2009), Moore *et al.* (2011), Torsvik *et al.* (2013), Warren *et al*. (2013)
Rodrigues	15		
Henderson	0.2	Pitcairn	Duncan et al. (1974), Clouard & Bonneville (2005), Neall & Trewick (2008), best estimate for Henderson (composed entirely of coralline limestone)
Pitcairn	1		
Clarion	4.5	Revillagigedo	Bryan (1966), Farmer *et al.* (1993), Bohrson & Reid (1998), Triantis *et al.* (2016), best estimate for Socorro and Clarion.
Socorro	1.7		
Ofu	0.4	Samoan Islands	Natland (1980), Clouard & Bonneville (2005), Cameron *et al.* (2013)
Olosega	0.4		
Tutuila	1.6		
Gough	2.5	Tristan da Cunha	Miller (1964), Mcdougall & Ollier (1982), Chevallier & Verwoerd (1987), Maund *et al*. (1988), Hicks *et al*. (2012)
Inaccessible	6		
Nightingale	18		
Tristan da Cunha	0.2		

Table S5. Pearson correlation matrix for island age and archipelago configurations at different sea-levels: highest (SLH_{CA} and SLH_{CACI}), intermediate (SLI_{MED} and SLI_{FREQ}), and lowest (SLL_{-122} and SLL_{GM}). Each archipelago configuration consists of the following predictors: current area (CA), current isolation (CI), area change (dA), and palaeo–connectedness (PC). All correlations have a P value higher than 0.1 (significance levels: "." = P < 0.1, "" = P < 0.05, "**" = P < 0.01, "***" = P < 0.001).*

	Highest		Intermediate				Lowest			
	SLH_{CACI}		SL_{MED}		SL_{FREQ}		SL_{MIN122}		SL_{GM}	
	CA	CI	dA	PC	dA	PC	dA	PC	dA	PC
Age	**-0.03**	**0.21**	**0.20**	**0.02**	**0.16**	**-0.07**	**0.11**	**-0.17**	**0.10**	**-0.16**

Table S6. Pearson correlation matrix for archipelago configurations at different sea-levels: highest (SLH_{CA} and SLH_{CACI}), intermediate (SLI_{MED} and SLI_{FREQ}), and lowest (SLL_{-122} and SLL_{GM}). Each archipelago configuration consists of the following predictors: current area (CA), current isolation (CI), area change (dA), and palaeo–connectedness (PC). Significance levels: "." = P < 0.1, "" = P < 0.05, "**" = P < 0.01, "***" = P < 0.001.*

			Highest				Intermediate						Lowest					
			SLH_{CACI}				SL_{MED}				SL_{FREQ}				SL_{MIN122}		SL_{GM}	
			CA		CI		dA		PC		dA		PC		dA		PC		dA		PC
Highest	SLH_{CACI}	CA	1.00																		
		CI	-0.16		1.00																
Intermediate	SLI_{MED}	dA	0.74	***	-0.11		1.00														
		PC	0.03		-0.25	.	0.35	*	1.00												
	SLI_{FREQ}	dA	0.75	***	-0.16		0.96	***	0.33	*	1.00										
		PC	0.13		-0.24	.	0.44	**	0.80	***	0.49	***	1.00								
Lowest	SLL_{-122}	dA	0.79	***	-0.20		0.87	***	0.28	*	0.92	***	0.43	**	1.00						
		PC	0.21		-0.31	*	0.37	**	0.70	***	0.50	***	0.88	***	0.54	***	1.00				
	SLL_{GM}	dA	0.79	***	-0.20		0.87	***	0.28	*	0.92	***	0.43	**	1.00	***	0.54	***	1.00		
		PC	0.23	.	-0.33	*	0.38	**	0.67	***	0.51	***	0.86	***	0.55	***	0.97	***	0.54	***	1.00

Table S7. Standardized coefficients of linear mixed models for 53 volcanic oceanic islands in 12 archipelagos for land snails (SIE_S, N_S, MIE_S) and angiosperms (SIE_P, N_P). We fitted linear mixed models for archipelago configurations at different sea-levels: highest (SLH_{CA} and SLH_{CACI}), intermediate (SLI_{MED} and SLI_{FREQ}), and lowest (SLL_{-122} and SLL_{GM}). SLH_{CA} (current area only), CACI; current configuration (current area, current isolation), SL_{MED}; palaeo–configuration during median sea level, SL_{FREQ}; palaeo–configuration during most frequent sea level, SL_{MIN122}; palaeo–configuration at -122m MSL, SL_{GM}; palaeo–configuration at Last Glacial Maximum. Each model contains a selection of the following predictors: CA; current area, CI; current isolation, PC; palaeo–connectedness, dA; delta area. Significance levels: "." = P < 0.1, "" = P < 0.05, "**" = P < 0.01, "***" = P < 0.001.*

Archipelago configuration			SIE_S		SIE_P		N_S		N_P		MIE_S	
Highest	SLH_{CA}	CA	0.456	***	1.010	***	0.313	**	0.453	***	0.335	***
	SLH_{CACI}	CA	0.375	***	0.766	***	0.269	***	0.337	***	0.248	***
		CI	0.003		-0.110	*	0.069		-0.171	***	-0.197	*
Intermediate	SLI_{MED}	CA	0.282	***	0.744	***	0.175	.	0.387	***	0.255	***
		PC	-0.311	***	-0.359	***	-0.237	***	-0.009		0.021	
		dA	0.418	***	0.147	*	0.045		-0.047	*	0.167	.
	SLI_{FREQ}	CA	0.122	*	0.653	***	0.199	*	0.431	***	0.273	***
		PC	-0.359	***	-0.312	***	-0.180	*	0.067	***	0.036	
		dA	0.525	***	0.146	*	0.033		-0.105	***	0.185	.
Lowest	SLL_{-122}	CA	0.121	*	0.663	***	0.239	*	0.450	***	0.297	***
		PC	-0.375	***	-0.310	***	-0.114		0.078	***	0.074	
		dA	0.504	***	0.072		0.010		-0.174	***	0.052	
	SLL_{GM}	CA	0.194	***	0.708	***	0.250	**	0.430	***	0.287	***
		PC	-0.358	***	-0.252	***	-0.103		0.059	***	0.070	
		dA	0.496	***	0.009		-0.005		-0.146	***	0.052	

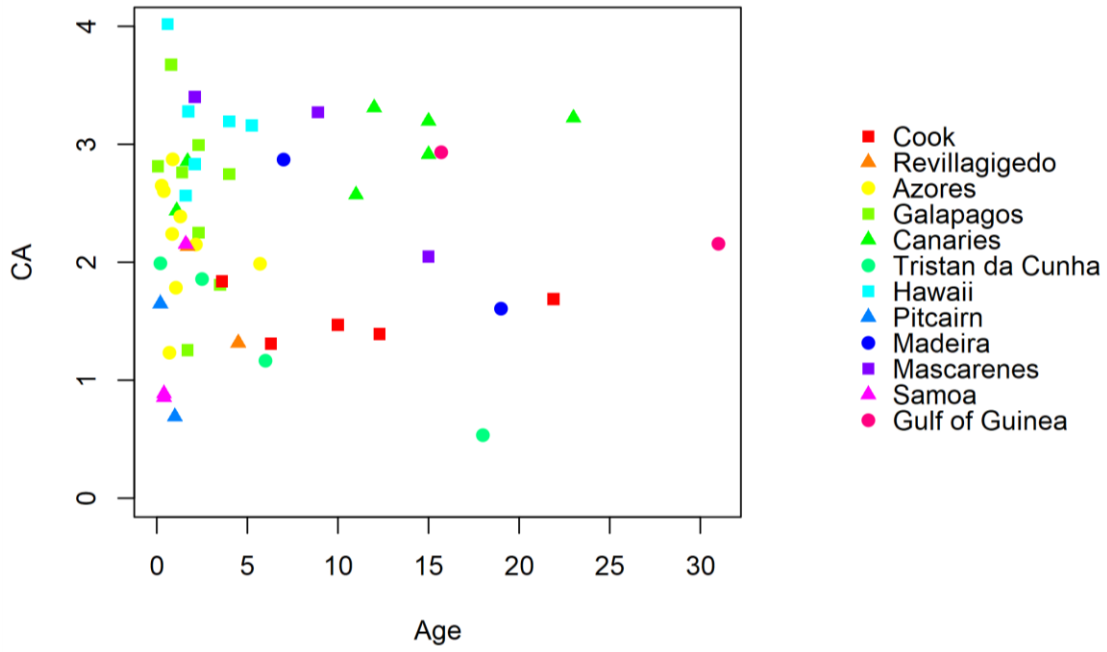

Figure S1a. Island age (Myr) and log-transformed current area (CA) for 53 islands in 12 archipelagos.

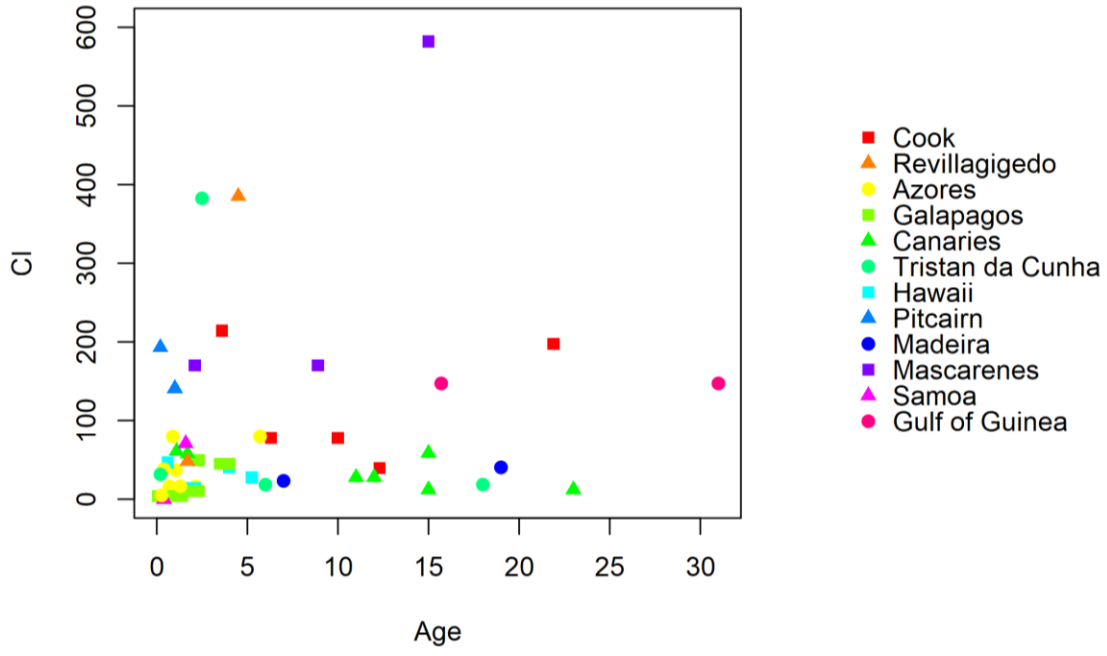

Figure S1b. Island age (Myr) and current isolation (CI) for 53 islands in 12 archipelagos.

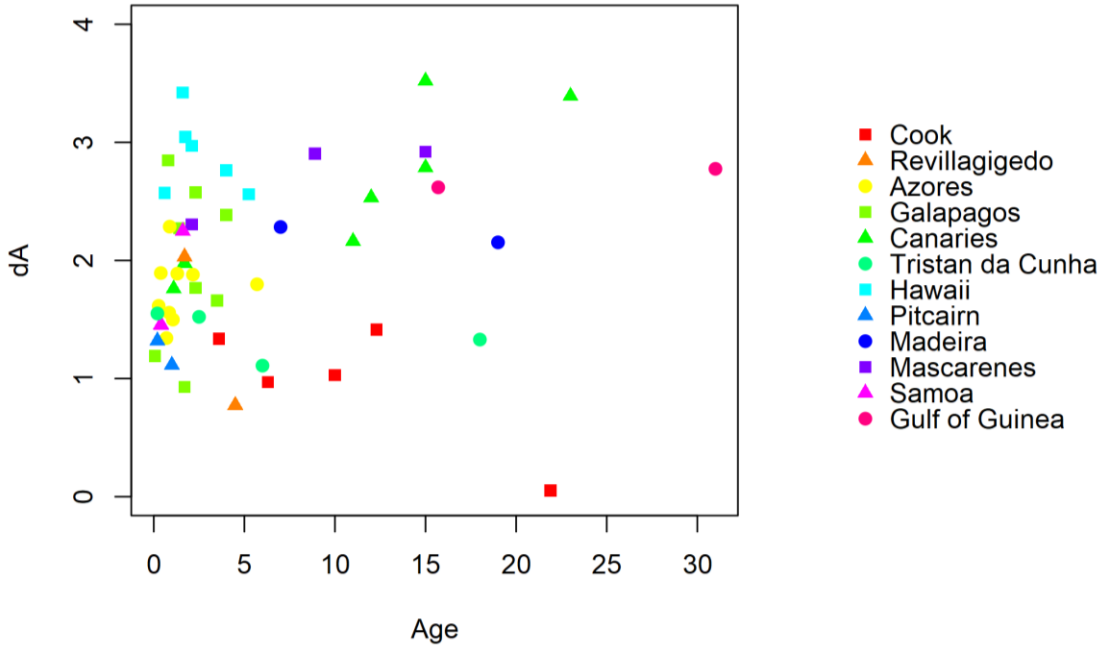

Figure S1c. Island age (Myr) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLI_{MED}.

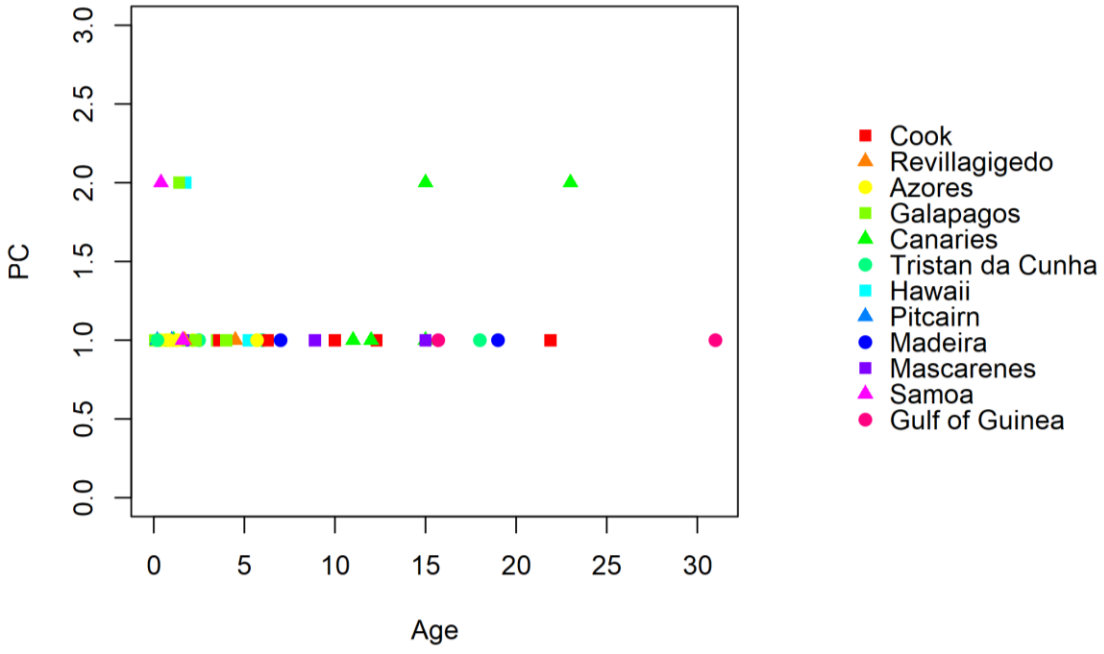

Figure S1d. Island age (Myr) and palaeo–connectedness (PC) for 53 islands in 12 archipelagos at SLI_{MED}.

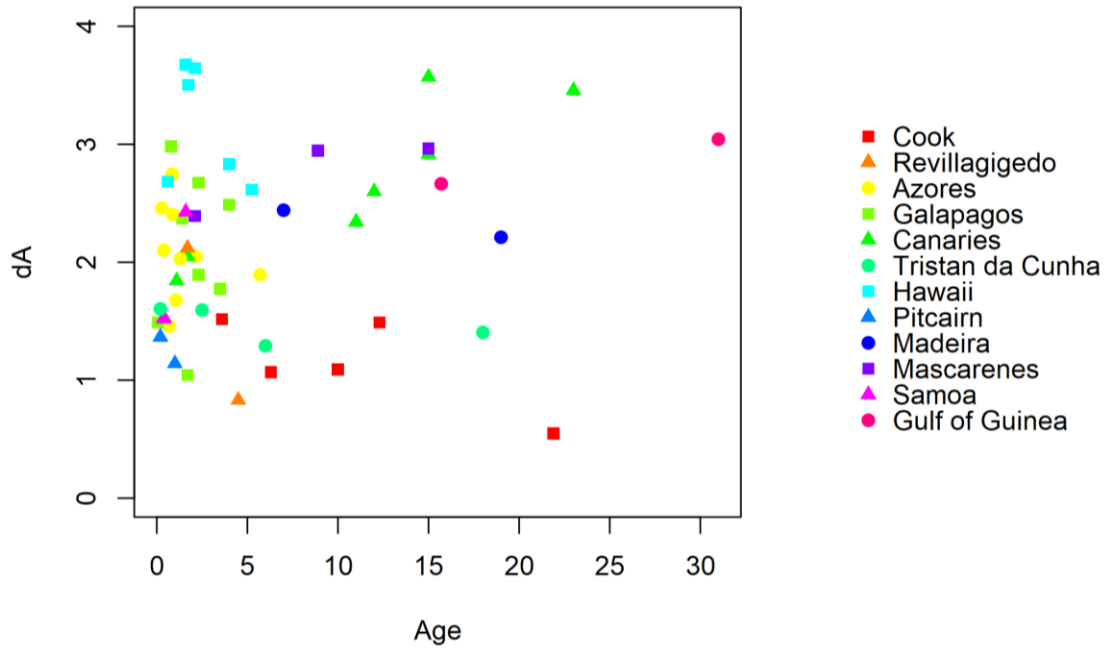

Figure S1e. Island age (Myr) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLI_{FREQ}.

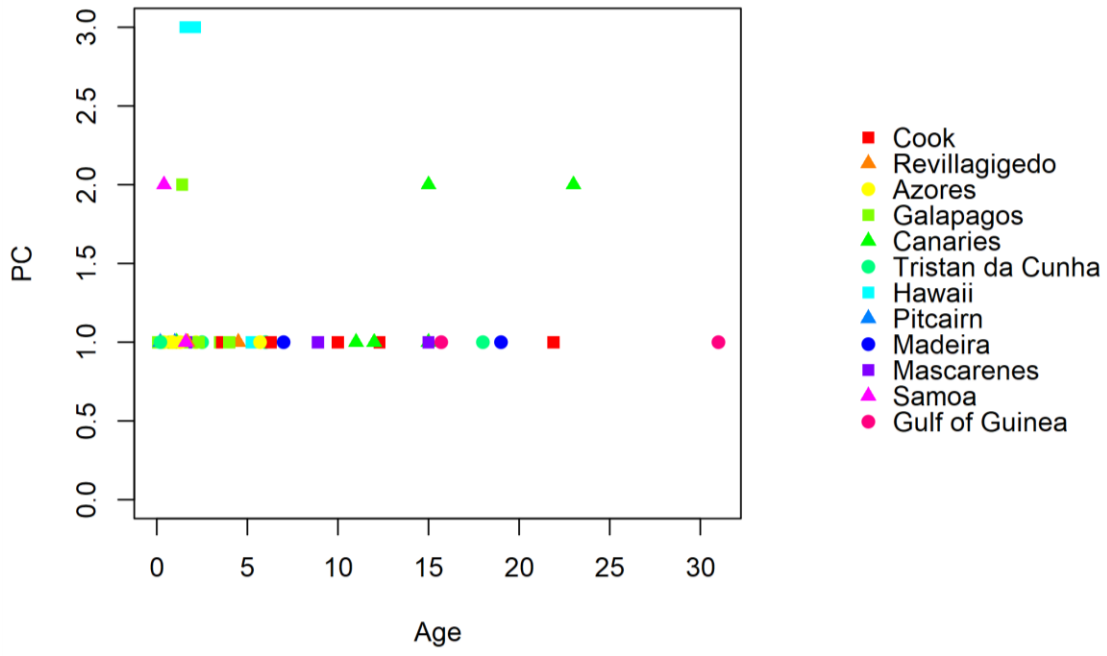

Figure S1f. Island age (Myr) and palaeo–connectedness (PC) for 53 islands in 12 archipelagos at SLI_{FREQ}.

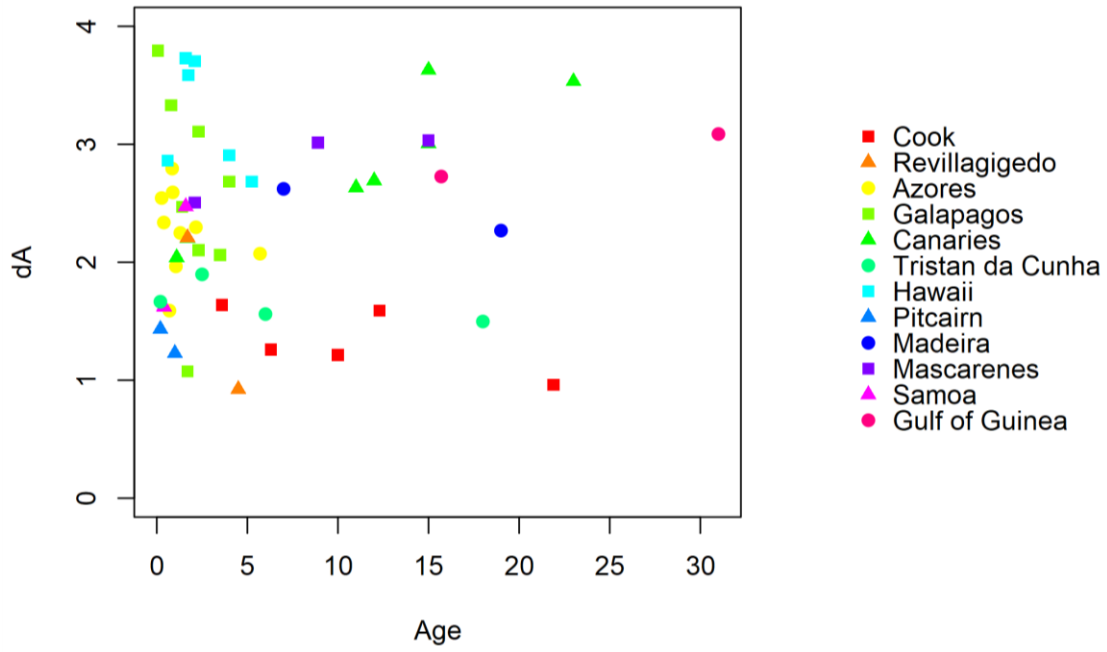

Figure S1g. Island age (Myr) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLL_{GM}.

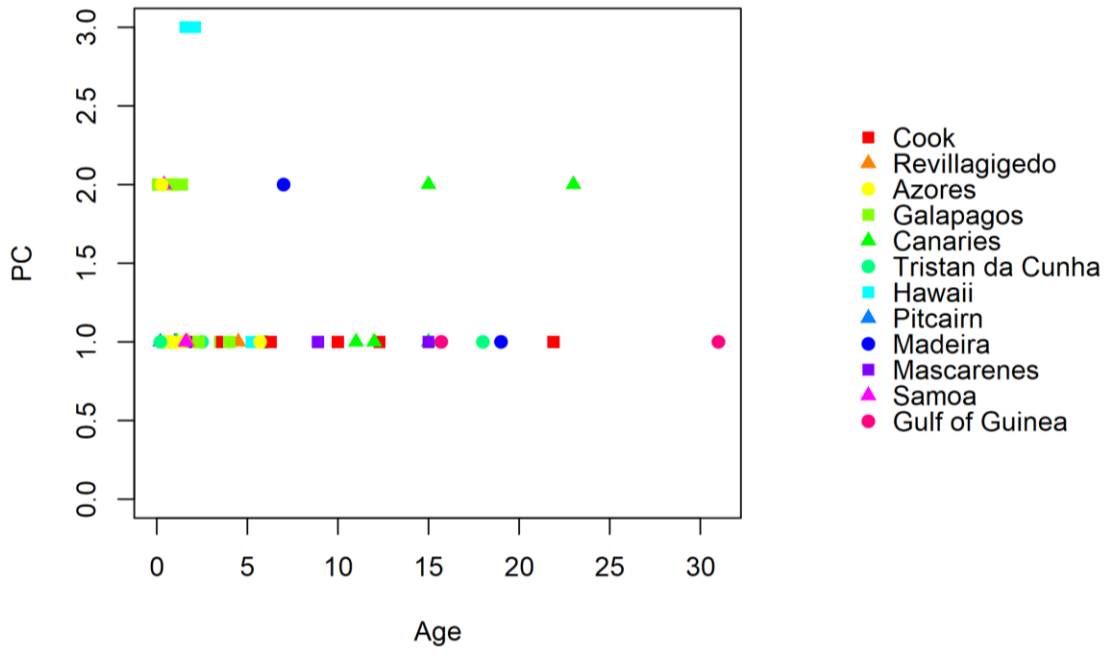

Figure S1h. Island age (Myr) and palaeo–connectedness (PC) for 53 islands in 12 archipelagos at SLL_{GM}.

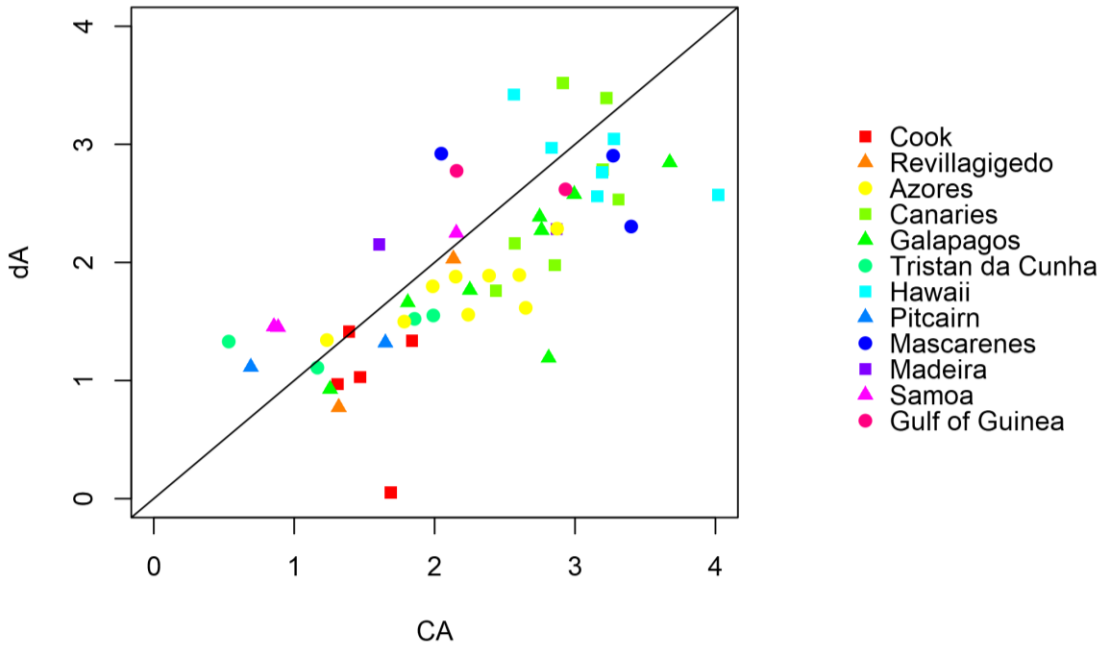

Figure S2a. Log-transformed current area (CA) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLI_{MED}.

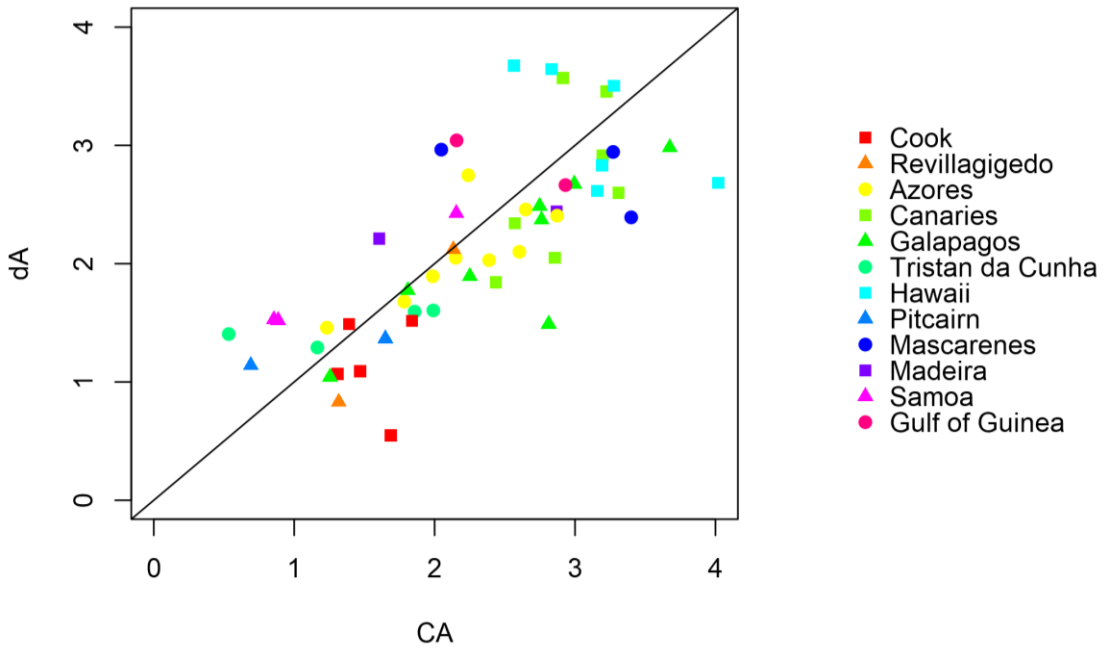

Figure S2b. Log-transformed current area (CA) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLI_{FREQ}.

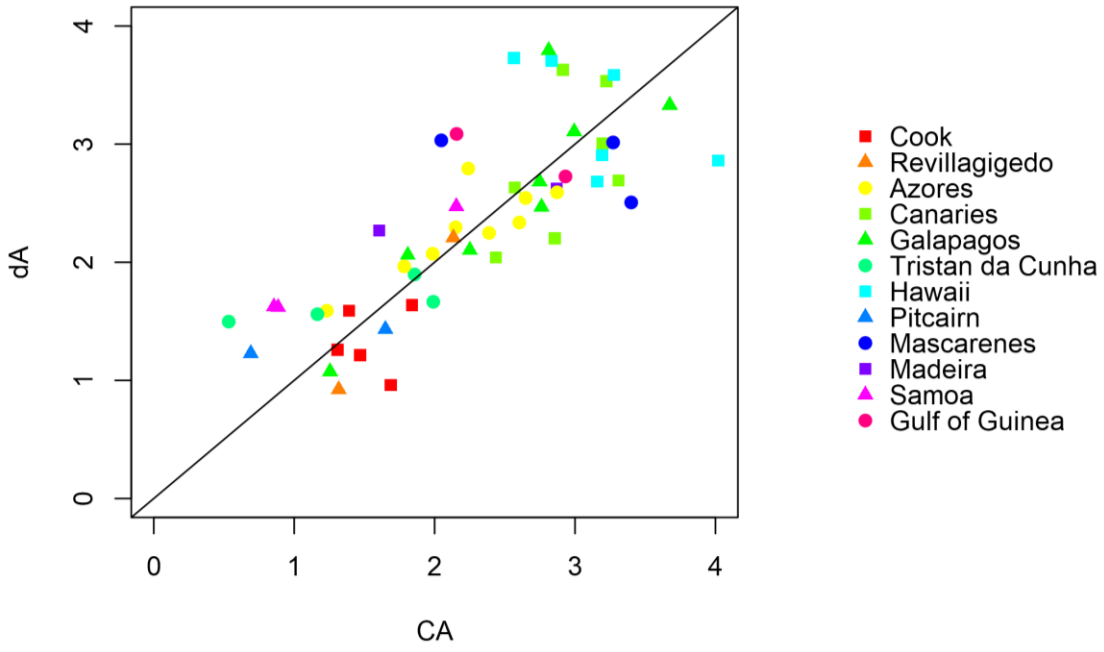

Figure S2c. Log-transformed current area (CA) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLL_{GM}.

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Appendices corresponding to section 2.1

Assessing temporal couplings in social-ecological island systems: historical land use change and soil loss analyses on Mauritius (Indian Ocean)

OVERVIEW OF APPENDICES

On the following pages you will find one appendix:

- Appendix 1, see also: https://www.ecologyandsociety.org/vol22/iss1/art29/appendix1.pdf

LINKS TO ONLINE SUPPORTING INFORMATION

The RUSLE model and input data are shared in the supplementary materials are shared on the website of Ecology & Society:

https://www.ecologyandsociety.org/vol22/iss1/art29/appendix2.zip

APPENDIX 1

Table A1.1. Overview of data transformations to develop RUSLE factors. All raster files have a cell size of 100x100 meters (1 hectare).

Factor	Input data	Transformation
R	Precipitation data from Mauritius Meteorological Services (2005) and Padya (1984).	For the calculation of pi, the monthly rainfall over 30 years between 1951 and 1980 from 23 stations was interpolated at a 100m resolution. The interpolation was conducted per month (thus resulting in 30 x 12 = 360 maps. Five interpolation methods were evaluated: linear, inverse distance weighted, cubic spline, generalized additive modelling in combination with kriging, and radial basis functions. Elevation, aspect and gradient were evaluated as covariates, along with x- and y-coordinates, in the interpolations. Only elevation appeared to be a meaningful covariate. The performance of each interpolation method was measured by calculating the root mean squared error through leave-one-out cross-validation (Hastie et al. 2009). Through this evaluation, the interpolation by radial basis functions turned out to be the best performing technique (rmsq = 79.9 mm), followed by inverse distance weighted interpolation (rmsq = 114.6 mm). Linear interpolation was the method with the lowest performance. The results from the radial basis function interpolation were used as average monthly precipitation (Pi) to calculate a modified Fournier index (F). Usually, the EI30 rainfall erosivity index (Wischmeier and Smith 1978) is used but in absence of rainstorm intensity data, it was replaced by the modified Fournier index (Arnoldus 1977, 1980) which linearly correlates with the rainfall erosivity index (Ferro et al. 1999). The modified Fournier index was calculated as follows: $F = \frac{\sum_{i=1}^{12} p_i^2}{P}$ where Pi = average monthly precipitation (mm) and P is the average annual precipitation (mm). Subsequently, the modified Fournier index was used to calculate an R factor for Mauritius: $R \quad rF^{a}$ where r and a are location specific parameters. We have used r = 0.00302 and a =1.9, following Arnoldus (1980), as cited by Le Roux et al. (2005).

K	Digitized vector map with spatial distribution of soil types from Willaime (1984). Soil erodibility factors from Nigel and Rughooputh (2012).	K values assigned. Digitized vector map converted to raster (100x100m).
LS	Digital Elevation Model (DEM) of Mauritius from (Seul 1999) and Hill (2001).	L is the length factor, λ the slope length (m) and m is the slope-length exponent (m = 0.5 on slopes >5°, 0.4 on slopes between 3° and 5°, 0.3 on slopes between 1° and 3°, 0.2 on slopes <1°). Slope length is normalized for a unit plot of 22.13m. $L = \left(\frac{\lambda}{22.13}\right)^{m}$ Slope steepness is calculated differently for slopes < 9° and for slopes ≥9°: $For\ S < 9°, S = 10.8\ sin\beta + 0.03$ $For\ S \geq 9°, S = 16.8\ sin\beta - 0.50$
P	Land use distribution for six time slices from Vaughan and Wiehe (1937) and references therein, and Page and D'Argent (1997). Support practice factor from Nigel and Rughooputh (2012).	P values assigned. Digitized vector maps converted to raster (100x100m).
C	Land use distribution for six time slices from Vaughan and Wiehe (1937) and references therein, and Page and D'Argent (1997). Cover management factor from Nigel and Rughooputh (2012).	C values assigned. Digitized vector maps converted to raster (100x100m).

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Appendices corresponding to section 2.2

Global change in microcosms: environmental and societal predictors of land cover change on the Atlantic Ocean Islands

OVERVIEW OF APPENDICES

On the following pages you will find one appendix.

LINKS TO ONLINE SUPPORTING INFORMATION

There is no link to online supporting information since the paper corresponding to section 2.2. has not yet been published. However, the data supporting the results presented in this section are also provided as part of the appendix.

APPENDIX

Table A.1. Sources for historic and modern demographic data per archipelago.

	Azores	Madeira	Canary Islands	Cape Verde	Gulf of Guinea
Sources	(Duncan, 1972; Sousa, 2013; SREA – Serviço Regional de Estatística dos Açores, 2016)	(De Oliveira, 2013; Direção regional de estatística da Madeira, 2017; Duncan, 1972)	(Godinho, 1952; ISTAC - Instituto Canario de Estadística, 2017)	(Duncan, 1972; Lindskog and Delaite, 1996; Wils, 1996)	(Eyzaguirre, 1986a; Garfield, 2018; INE - Instituto Nacional de Estatística, 2013; Lorenzino, 2007; Seibert, 2013).

Table A.2. Data on topography, climate, and society for the 30 Eastern Atlantic Islands. These data were used in the statistical analysis. Popdens: population density, landmod: landscape modification, natveg: native vegetation. Data sources are explained in the main text.

island	archipelago	ruggedness	area	elevation	temperature	precipitation	popdens	landmod	natveg
Corvo	Azores	10.29	17	718	17.1	1405.9	25	0.15	51.3
Faial	Azores	4.56	173	1043	17.0	1325.3	87	0.41	9.4
Flores	Azores	7.17	143	914	16.8	1646.5	27	0.18	32.9
Graciosa	Azores	3.87	61	402	17.3	1132.0	72	0.47	0.4
Pico	Azores	4.75	446	2351	16.7	1357.9	32	0.23	13.7
S. Maria	Azores	4.48	97	587	17.2	823.0	57	0.45	7.8
S. Jorge	Azores	6.81	246	1053	16.8	1323.5	37	0.29	14.7
S. Miguel	Azores	4.98	757	1103	16.7	1071.6	182	0.47	8.7
Terceira	Azores	3.31	401	1021	17.3	1199.2	141	0.39	14.2
El Hierro	Canary Islands	7.81	278	1501	18.2	294.5	38	0.28	53.0
Fuerteventura	Canary Islands	4.06	1725	807	20.0	128.6	64	0.31	13.0
Gran Canaria	Canary Islands	7.97	1532	1950	18.0	265.4	550	0.45	48.0
La Gomera	Canary Islands	11.39	378	1487	17.9	309.2	55	0.31	70.0
La Palma	Canary Islands	9.51	729	2423	16.2	402.7	112	0.30	69.0
Lanzarote	Canary Islands	3.38	796	671	19.5	145.7	185	0.39	36.0
Tenerife	Canary Islands	6.34	2058	3718	16.0	359.0	435	0.41	55.0
Boa Vista	Cape Verde	2.28	620	390	23.4	71.1	25	0.16	17.5
Brava	Cape Verde	10.06	64	976	20.2	280.4	88	0.53	48.4
Fogo	Cape Verde	7.17	476	2829	18.9	360.0	75	0.30	42.0
Maio	Cape Verde	1.95	269	436	24.3	160.4	26	0.20	32.9
Sal	Cape Verde	1.61	216	406	23.2	70.0	163	0.26	3.7
Santiago	Cape Verde	7.26	991	1392	22.9	268.5	301	0.47	44.4
S. Antao	Cape Verde	10.64	779	1979	20.6	300.3	51	0.24	46.2
S. Nicolau	Cape Verde	8.53	343	1304	21.9	198.3	36	0.29	38.6
S. Vicente	Cape Verde	6.17	227	774	23.5	125.2	361	0.35	10.6
Annobón	Gulf of Guinea	10.65	17	598	18.3	2063.6	308	0.29	47.5
Príncipe	Gulf of Guinea	6.63	136	947	24.6	2167.3	54	0.22	61.1
S. Tomé	Gulf of Guinea	8.05	854	2024	22.6	2518.5	201	0.25	57.8
Madeira	Madeira	11.47	741	1850	15.2	716.1	338	0.42	42.0
Porto Santo	Madeira	5.83	43	517	18.3	431.5	120	0.62	0.0

Table A.3. Biodiversity Change and Current Status per Archipelago.

Azores. The Azorean Islands were largely covered by dense forests at the time of discovery (Dias, 2007; Frutuoso, 1589a, 1589b, 1589c). Laurel forest (lowland and sub montane forests), with tall trees was likely the most dominant forest type (Costa, 1950; Elias et al., 2016; Rull et al., 2017a). Human activities, including burning, cattle ranging, and land conversion, caused a rapid shift in native vegetation from dense forests to open scrublands (Connor et al., 2012; Rull et al., 2017b). On the Azores, native forests are currently restricted to less than 5% of the archipelago area, completely absent in Graciosa and Corvo and with larger areas being mostly present in Terceira, Pico and Flores, that include also the fragments with the highest index of biotic integrity (Gaspar et al., 2011). Although the trees in these remaining forest patches do not seem to be able to reach their maximum height, the canopy biota is still dominated by native non-endemic and endemic arthropods (Borges et al., 2008), with large number of endemic spiders (Florencio et al., 2016). Owing to the high humidity, large parts of the islands are covered with mosses and liverworts (Gabriel and Bates, 2005; Sjögren, 1978). In contrast to the other archipelagos, large peat formations are also present on the Azores (Allorge and Allorge, 1946; Mendes and Dias, 2017). The majority of the introduced plant species on the Azores are ornamental or have a non-food use value (aromatic, animal fodder, or hedge-plants), only a small fraction is suitable for human consumption (Silva and Smith, 2004). With exception of bats, all the remaining mammals from Azores are introduced. Confirmed extinctions of invertebrates in Azores (Cardoso et al., 2010; Terzopoulou et al., 2015) and the high percentage of currently threatened beetles (Borges et al., 2017) are good indicators of massive biodiversity erosion in Azores. However, there are also examples of native insects which were able to successfully colonize anthropogenic habitats as is the case of native flower-visiting insects that are also pollinating exotic plants (Picanço et al., 2017), promoting their spread. In contrast, there are also situations in which introduced pollinators provide ecological "insurance" helping the pollination of native plants (Weissmann and Schaefer, 2017).
Madeira. Early descriptions of Madeira mention dense laurel forests composed mostly by trees which covered almost the entire islands (Frutuoso, 1589d; Gomes, 1500). Madeira and Porto Santo forests possibly included several vegetation belts more or less similar to the ones described by Capelo et al. (2004): a Mediterranean vegetation belt (lower part dominated by *Olea maderensis*, *Dracaena draco*, *Syderoxylon mirmulans* and other small trees, and an upper part dominated by laurel and barbusano forest), a temperate vegetation belt (with a lower part dominated by laurel and *Apollonias barbujana* forest and a upper part dominated by *Ocotea foetens*), the upper summits were possibly dominated by a tall forest of *Juniperus cedrus* and *Erica arborea*. Madeira archipelago forests contained at least 20 species of trees but possibly there have been some extinctions during the first centuries of human colonization (Jardim et al., 2007; Jardim and Menezes de Sequeira, 2008; Menezes de Sequeira et al., 2007). On Madeira archipelago, the remaining native vegetation is almost exclusively located on the island of Madeira (737.5 km^2) while the much smaller island of Porto Santo (42 km^2) has virtually no remaining natural vegetation (Menezes de Sequeira et al., 2007). The main drivers for removal of native vegetation were deforestation, and herbivory by rabbits (*Oryctolagus cuniculus*), feral goats (*Capra hircus*), and cattle (Eanes da Zurara, 1473; Frutuoso, 1589d). On Porto Santo, several tree species known from historical descriptions were already extinct prior to scientific (Linnaean) descriptions of the island's vegetation. Although on Madeira island there is a lack of evidence for tree extinctions/extirpations, six extirpations (native and Macaronesian endemics) are registered. In addition, historical documents prior to 1753 seem to support the pre-Linnean extinction of one tree species (Jardim and Menezes de Sequeira, 2008). Habitat destruction has resulted in the extinction of nine land snails since human settlement (Goodfriend et al., 1994).
Canary Islands. Of the Canary archipelago, 99% was covered by vegetation; although potential vegetation models suggest that only 40% was forest (del Arco Aguilar et al., 2010). The native ecosystems include, from coast to summit, coastal scrublands, thermophilous woodlands, evergreen laurel forests, pine forests and summit scrublands. On average, the Canary Islands have a large remaining native vegetation cover, although from the first centuries after the Castilian conquest most forests experienced a sharp reduction. Intensive forest exploitation with no systematic management, along with intentional fires, expansion of monocultures and overgrazing, resulted in composition changes and strong fragmentation

(Parsons, 1981). In the last centuries the pine forest has been largely reforested, while the abandonment of agricultural land has prompted a steady recovery of the laurel forest and the expansion of the coastal scrubland in old fields. The exception is the thermophilous woodland with less than 10% of its original area remaining (del Arco Aguilar et al., 2010). Many endemic plant species are endangered and survive on isolated and inaccessible areas away from human pressure and introduced herbivores. The introduction of commensal species in (pre-) historic times, especially the house mouse, rats and cats, were among the main causes of (local) extinction of endemic rodents, birds, and possibly lizards (Rando, 2003; Rando et al., 2014, 2011), by hyper-predation, competition, acting as a vectors of diseases and direct predation. Some of the bird extinction events may have been initiated by hunting during prehistoric settlement, however, most bird extinctions concluded upon the arrival of Europeans (Illera et al., 2012). Goats and sheep, brought by the first settlers and rabbits later by Europeans, greatly affected the native vegetation by grazing and browsing. In addition, the decline and disappearance of some trees (e.g. *Carpinus* and *Quercus* from Tenerife) was likely also caused by the first settlers (de Nascimento et al., 2016, 2009). In order to preserve the remaining natural areas and their biodiversity, various forms of protection have been established: the Canarian Network of Natural Protected Areas, including four National Parks, and covering around 40% of the territory, the European Union Natura 2000 Network, several UNESCO protection figures, and National Marine Reserves, and the catalogues of endangered species.

Cape Verde. Early descriptions of the Cape Verde Islands following human colonization mention the scarce number of trees and the limited productivity of the land (Pereira, 1533). Although few trees grew on the islands, early descriptions also mention the presence of productive fig trees (*Ficus* spp.) and of dragon trees (*Dracaena draco* subsp*. caboverdeana*) (Gomes, 1500). Since the islands were colonized in the 15th century, cattle-raising, agricultural practices, and wood collection have affected the extent and composition of native scrublands, and two plant species possibly went extinct (Romeiras et al., 2016). In the highlands of Santiago, overgrazing and native vegetation removal led to sustained erosion and soil degradation, a context in which invasive species spread (Castilla-beltrán et al., 2019). Presently, the mountain areas are dominated by exogenous tree species introduced for afforestation (e.g. *Pinus canariensis*), a dense endemic scrublands (e.g. *Euphorbia tuckeyana*) and some scattered endemic (e.g. *Sideroxylon marginatum* and *Dracaena draco* subsp*. caboverdeana*) and native trees (e.g. *Ficus* spp.), while in the lowlands, herbaceous species and some native xeric trees (e.g. *Faidherbia albida* and *Tamarix senegalensis*) occur (Romeiras et al., 2014; van Gils, 1998). Studies on Cape Verde are generally biased towards specific taxa with many of them still understudied, especially among the insects. Most studies focused on reptiles and plants (Romeiras et al., 2019), while some others also deal with invertebrates, like butterflies (Tennent and Russell, 2015). The conservation status and threats of the endemic vascular flora (Romeiras et al., 2016) and reptiles (Vasconcelos et al., 2013) were recently reviewed. These studies have shown that most of the endemic species are classified in one of the IUCN threat categories (i.e. CR, EN and VU). Among the reptiles, *Chioninia coctei* was last seen in 1912, and was listed as extinct by IUCN (Schleich, 1996). Also the remains of a land tortoise have been found in Quaternary deposits on Sal Island, and was identified by Chevalier (1935) as being similar to those of a *Geochelone sulcate* (syn. *Centrochelys sulcata*). In fact, those remains are from a close but distinct species, *Geochelone atlantica* (López-Jurado et al., 1998) which was considered extinct. During the last 12 years, several conservation actions were undertaken by the Cape Verde authorities, in particular establishing a system of Protected Areas to safeguard the natural heritage of the archipelago (MAAP, 2014).

Gulf of Guinea. Around the time of human colonization, the islands of the Gulf of Guinea were almost entirely covered by forest (BDPA, 1985; Exell, 1944; Figueiredo et al., 2011; Henriques, 1917; Salgueiro and Carvalho, 2001; Soares, 2017). Today, around one quarter of the archipelago is still covered by native forest, which is currently surrounded by a similar extent of secondary forest. Both these forests persist in the most mountainous portions of the islands, mostly located in their centre and south (Jones et al., 1992). The endemic-rich native biodiversity is heavily reliant on native forest, even though they can often use secondary forest and, to a lesser extent, plantations, especially when these maintain a dense canopy cover. Widely distributed species are strongly associated to anthropogenic land covers, while the

endemics are either distributed across the islands or prefer forest ecosystems (de Lima, 2012; de Lima et al., 2013; Soares, 2017). Many species have been introduced in these islands (Dutton, 1994; Figueiredo et al., 2011; Jones and Tye, 2006), but the exact extent of these introductions and their impact on native ecosystems is still poorly understood (de Lima et al., 2014). Only one extinctions has been recorded: a crocodile (Ceríaco et al., 2018), even though this might be due to the scarcity of records and lack of paleontological studies. Very little is known about most invertebrate groups (Jones, 1994). Many species are considered threatened and anthropogenic pressure on the unique biodiversity of these islands is expected to continue, namely in the form of land use change, overexploitation and introduced species (IUCN, 2018; Jones and Tye, 2006).

Table A.4. Historic socioeconomic trends in the Azores.

Century	Agricultural production for local consumption and export and trade
14th century and before (until 1400)	There is recent evidence of human presence in Azores prior to the Portuguese settlement in the 15th century (Jones et al., 2013; Rodrigues et al., 2015; Rull et al., 2017b); based on a 700-year pollen record from São Miguel Island (Caldeira of Sete Cidades), there is evidence of human disturbance in the period 1300-1400, culminating with local deforestation that is manifested by local forest burning, cereal cultivation and possibly animal husbandry (Rull et al., 2017b).
15th century (1400-1500)	European workers subsistence farming (peasants, farmers) (Thornton, 2012); the Azores were important producers of wheat for the Portuguese crown and for trade with Morocco (Almeida et al., 2011); 1450 introduction of sugar cane in São Miguel and Santa Maria but soon ceded; end of century: blue-dye pastel (woad) backbone of economy for next 1.5 century (Greenfield, 1979); 1490 pastel (Duncan, 1972)
16th century (1500-1600)	Whole century blue-dye pastel main commodity; wheat (Duncan, 1972; Silveira, 2007); 1540 reintroduction of sugar cane to São Miguel (Greenfield, 1979).
17th century (1600-1700)	Staple exports: wheat, pastel and flax (including derived products linen and cloth), wheat for export, peasantry was eating maize and yams (Duncan, 1972); export of several products, import of sugar from Brazil. Pico wine (Duncan, 1972); 1685 end of pastel (peak importance 1550-1650), outcompeted by indigo from Brazil (Duncan, 1972). 1620-1694: decrease in pastel, increase in linen; also inter-island trade: products embroideries, bacon, 1640 onwards broad beans, 1646 onwards: barley, export of pork products (Duncan, 1972).
18th century (1700-1800)	±1740 end of blue-dye pastel? Diversity of crops; throughout the centuries: many crops of local importance: sweet potatoes, yams, potatoes, grapes, beetroot, tea, peanuts, tobacco, etc.; also fishing, whaling, cattle, sheep, dairy products; but all export products economically insignificant (Duncan, 1972).
19th century (1800-1900)	First record of foot rot in citrus trees was recorded on the Azores in 1834, in following decades decay of orange plantations (Grant et al., 1953). Despite the orange disease, the industry continued to prosper during the first half of the 19th century but started to deteriorate in the 1870s (Carvalho Benevides, 2013); during 1890-1895 orange groves devastated/destroyed; Pico wine (Duncan, 1972); end of 19th century: corn replacing wheat.
20th century (1900-2000)	1960: cattle grazing; rapid deforestation at mid- and higher elevations during (and after) WWI and WWII; 1950 reforestation with fast-growing exotic species; 1970-1990 deforestation for pastures at high elevations.

Table A.5. Historic socioeconomic trends in Madeira.

Century	Agricultural production for local consumption and export and trade
14th century (1300-1400) and before	
15th century (1400-1500)	1420s: rabbits, cows, pig, sheep introduced to the islands prior to human settlement (Moore, 2009a); hardwood cutting and exportation (28, and references therein); 1430s-1450s: cattle raising, export of cereals (mainly wheat) (Almeida et al., 2011) and wood; introduction of many cultivated plants including vine; sugar cane became commercially viable in 1450, in the early 1470s there was a rapid increase of sugar cane production (9-fold increase between 1472 and 1506) and deforestation (Moore, 2009a, 2009b); reduction of cereal production; Introduction of European crops (including *Castanea sativa*, *Citrus*, *Ficus*, *Prunus*, etc.).
16th century (1500-1600)	Sugar production rose rapidly and peaked around 1506, and subsequently plummeted by 90% between 1506 and 1530 (Moore, 2009b, 2009a); 1540 wood shortages, not enough for sugar production; legal documents and laws to reserve part of forest to keep sugarcane production and export.
17th century (1600-1700)	Local agriculture focused on cash crops (grapes), high reliance on food imports (Duncan, 1972). 1650 cheap wine (Duncan, 1972); by the end of the 17th century 90% of export value from wine (Duncan, 1972).
18th century (1700-1800)	1703: Cheap wine (Hancock, 1998); introduction of new-world crops, possibly sweet potato, guavos (*Psidium guajava*), reference to Colocasia esculenta cultivation, possibly also mango (Mangifera indica), corn (*Zea mays*), *Opuntia*, etc. (Menezes de Sequeira et al., 2010).
19th century (1800-1900)	1807: luxury wine (Hancock, 1998). 1815 peak of wine trade (Hancock, 2005); wine production affected first by powdery mildew (caused by Oidium fungus) and later by Wine Blight (caused by Phylloxera aphids). 1840 elite wine (Duncan, 1972); slow return of sugar cane but affected by new diseases (second half of the 19th century), end of 19th century sugar cane plantations increase.
20th century (1900-2000)	Steady increase in sugar cane, increase in wine production, banana plantations, decrease in cattle, eradication of feral goats and mountain use for grazing, second half of century with a decrease in agricultural landscape (process ending in 2004).

Table A.6. Historic socioeconomic trends in the Canary Islands.

Century	Agricultural production for local consumption and export and trade
14th century and before (until 1400)	The initial settlers of the Canary Islands raised goats, sheep and pigs, and also gathered seafood. Crop cultivation was focused on cereals such as wheat and barley (Morales et al., 2009).
15th century (1400-1500)	This century coincided with the Castilian conquest of the Canaries (1402-1496); in the early-conquered islands (Lanzarote, Fuerteventura, La Gomera and El Hierro) a new agriculture was imposed, mainly based in cereals (Morales et al., 1992); in the late-conquered islands (Gran Canary, La Palma and Tenerife) the agriculture/goat and sheep raising model persisted until the end of the century (Morales et al., 1992).
16th century (1500-1600)	Subsistence agriculture coexisted with cycles of exportation monocultures: sugar cane became important in early 16th century (Mintz, 1986; Morales et al., 1992); end of 16th century sharp decline of sugar cane and emergence of wine (Parsons, 1981); as sugar decreased less wood needed for sugar mills (Parsons, 1981); 1593 peak in production of pitch (made from pine trees) (Parsons, 1981). Rain fed cereal cultivation for local consumption was relatively important during the 16-17th century.
17th century (1600-1700)	Subsistence agriculture coexisted with cycles of grape monocultures to produce wine for export (Morales et al., 1992). Rain fed cereal cultivation for local consumption was relatively important during the 16-17th century.
18th century (1700-1800)	Subsistence agriculture; agricultural-pastoral sector: maize, potatoes and domestic animals coexisted with a commercial export sector owned by foreigners; export economy was based on “orchilla” (*Rochella canariensis*) dyestuff, sugar, wine, “barilla” (*Mesembryanthemum crystallinum*) for caustic soda (Parsons, 1981); export of wood and shortage of hardwood (Parsons, 1981).
19th century (1800-1900)	Subsistence agriculture coexisted with cycles of exportation monocultures: banana and tomatoes (Morales et al., 1992). Halfway the 19th century there was a surge in the production of crimson dye, a natural colorant extracted from *Dactylopius coccus* (Hemiptera) insects living on the leaves of *Opuntia* spp. (introduced from Mexico with this purpose). Fires destroyed part of forest and regeneration was inhibited by livestock browsing (Parsons, 1981); attempts/mentioning of reforestation (Parsons, 1981).
20th century (1900-2000)	Subsistence agriculture coexisted with cycles of exportation monocultures: banana and tomatoes (Morales et al., 1992; Parsons, 1981); decreasing importance of local food crops due to agricultural abandonment following the tourist boom in the 1960s; intense reforestation programs (Parsons, 1981); establishment of national parks and reserves.

Table A.7. Historic socioeconomic trends in Cape Verde.

Century	Agricultural production for local consumption and export and trade
14th century and before (until 1400)	
15th century (1400-1500)	It has been suggested that horse breeding and cotton plantations were practiced since the late 1470's, with already some slave trade taking place (Green, 2011, p. 100).
16th century (1500-1600)	Experiments with sugar cane but on a smaller scale than Madeira, not a real sugar plantation economy as Madeira or São Tomé (Greenfield, 1979); plantation economy. Sugar cane and cotton, maize and beans also cultivated at smaller scales (Green, 2011; Havik et al., 2018). African slaves but perhaps also free people/refugees from Senegal (Baker, 2006; Thornton, 2012); cotton was traded for slaves along Guinea coast (Greenfield, 1979; Williams, 2015); salt export (15th – 20th century); For richer seafarers supply of some fruits, vegetables, and fresh meat (Duncan, 1972). Salt export (15th – 20th century); centre for collection and distribution of products for West Africa (Duncan, 1972). Most of the staple food crops for local consumption had to be imported (Fêo Rodrigues, 2008).
17th century (1600-1700)	Peak of slave trade (Duncan, 1972; McColl, 2014); meagre exports, lack of products. Export of sea salt; supply to ships (beverages, food: goat meat), not cargo. Salt export (15th – 20th century); provisioning of ships more dependable and regular economic activity than slave trade (Duncan, 1972). Importance as entrepôt market for transshipment of diverse commodities ceased (Romeiras et al., 2014); trade in cotton textiles (*pano*) for African elite (Heckman, 1985; Moran, 1982), weaving was done by slaves on Cape Verde, the clothes were traded for other slaves (Duncan, 1972; Moran, 1982; Williams, 2015).
18th century (1700-1800)	Cash crops not very successful until 19th century (Moran, 1982); 16th through 18th century: cotton and indigo for export (Duncan, 1972; Kriger, 2005); beginning of 18th century orchilla for textile colouring (Pereira, 2015) but ended in 1837 when it was discovered in Angola and Mozambique (Duncan, 1972); salt export (15th – 20th century).
19th century (1800-1900)	After abolition in 1880 subsistence agriculture, mainly maize (Wils, 1999); Beginning of 19th: cease of slave trade (Baker, 2006), followed by provisioning of ships; 1850: Storage depot of water and coal (fossil coal, not mined on the islands themselves) for long range ocean ships towards Americas (Wils, 1999); goat skins; salt export (15th – 20th century).
20th century (1900-2000)	Subsistence agriculture of corn, also beans and fish (Wils, 1999); Mid-20th century: afforestation projects to provide firewood, fodder, rural development and prevent soil erosion (Amaral, 1964); salt export (15th – 20th century); coal importance decreased towards end of 20th century.

Table A.8. Historic socioeconomic trends in the Gulf of Guinea.

Century	Agricultural production for local consumption and export and trade
14th century and before (until 1400)	
15th century (1400-1500)	1485 introduction sugar cane to São Tomé (Greenfield, 1979); initial forest clearance and establishment of first sugar cane plantations, mostly in dry coastal areas (Eyzaguirre, 1986b, 1986a); end of century marked by food shortages and food import, first domestic animals and food crops were introduced, mortality due to tropical diseases was a major challenge for settlement (Seibert, 2013).
16th century (1500-1600)	Sugar cane plantation economy (Greenfield, 1979); initially, the growth of sugar production was slow but it took off around 1510; slave revolt in 1517 (Garfield, 2018); lack of food between 1531 and 1535, and many slaves escaping from the plantations by mid-century (Seibert, 2013); 1540s-1570s: São Tomé at sugar cane commodity frontier (Moore, 2009a); massive slave revolt in 1595, most sugar mills destroyed (Garfield, 2018; Seibert, 2013); former slaves and their descendants rule the island (Garfield, 2018); by the end the century, the Dutch, French and English end the Portuguese monopoly in the region (Seibert, 2013); sugar production peaks in third quarter of the 16th century, followed by decline (Seibert, 2013). By 1580 there is a major exodus of investors to Brazil (Garfield, 2018); the Dutch raid the islands in 1599 (Seibert, 2013).
17th century (1600-1700)	Continued decline of the sugar cane plantations leads to the appearance of secondary forests, European administrative presence weakens, and subsistence farming emerges at higher elevations (Eyzaguirre, 1986b, 1986a). São Tomé and Príncipe were key slave trading posts. Trade with slaving boats maintained the local elite and some reliance on imports (Eyzaguirre, 1986a).
18th century (1700-1800)	European administrative presence remains weak, the “gleba” agroforestry system develops both in lowland and highland, based on tree and root crops grown in dense mixed stands with minimal tillage (Eyzaguirre, 1986a, 1986b). São Tomé and Príncipe were key slave trading posts. Trade with slaving boats maintained the local elite and some reliance on imports (Eyzaguirre, 1986a).
19th century (1800-1900)	Coffee is introduced in 1800 (Eyzaguirre, 1986a, 1986b), and cocoa in 1822 (Garfield, 2015); the “gleba” agroforestry system expands to supply the impoverished local population, while the Portuguese re-imposed their authority between 1858 and 1878, and start clearing large extents of forest to plant coffee and cocoa, in the intensive agroforestry “roça” system (Eyzaguirre, 1986a, 1986b); slavery is formally abolished in 1858, but by 1875 contracted workers are still fighting for freedom (Lorenzino, 2007).
20th century (1900-2000)	At the start of the century, the “roça” system expands, based on contract labor from Mozambique and Angola (Eyzaguirre, 1986a, 1986b), and confining native forest to a quarter of its original size (Jones et al., 1992); by 1910, cocoa production peaks, and these islands become the world’s leading cocoa producer. Other export crops, such as coffee, quinine and cinnamon, also expand. The “gleba” supplies only part of the food, while the “roças” remain highly reliant on food imports. Before 1935, competition with other African regions leads to the decline of the “roça” system and to the appearance of large extents of secondary forests. Increased production of food crops for local consumption, like potatoes, maize, annuals, cabbage, beans and carrots, but overall reliance on imports persists (Eyzaguirre, 1986a, 1986b).

Table A.9. Variance Inflation Factors (VIF) for all variables in the full model. Variables are scaled. Popdens: population density, Landmod: landscape modification.

	VIF
Ruggedness	1.43
Area	2.52
Elevation	2.23
Temperature	1.46
Precipitation	1.31
Popdens	1.95
Landmod	1.62

Table A.10. Regression coefficients of Partial Least Squares Regression analysis using the first two components. The data has been scaled - so coefficient values can be compared directly. Popdens: population density, Landmod: landscape modification.

	Natural Vegetation
Ruggedness	0.598
Area	0.084
Elevation	0.304
Temperature	0.180
Precipitation	0.051
Popdens	0.023
Landmod	-0.300

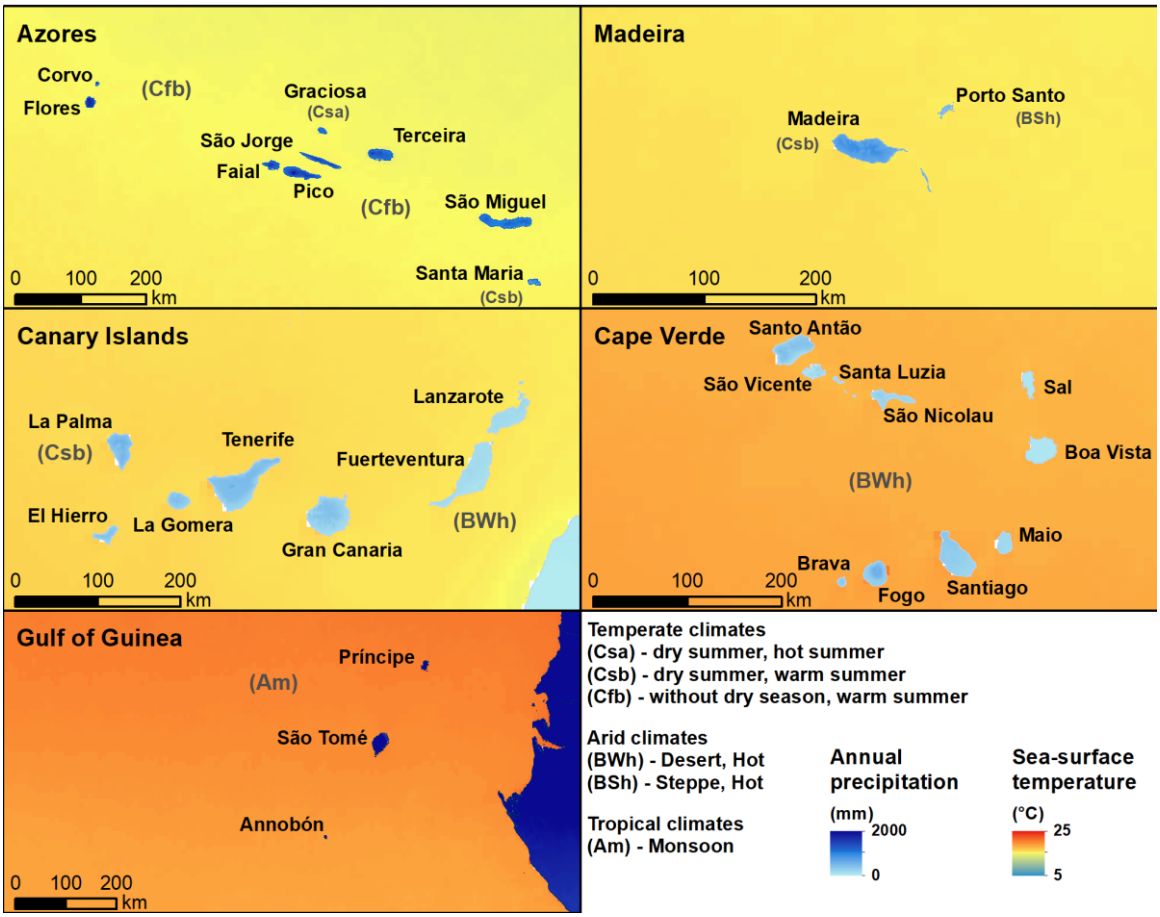

Figure A.1. Climatic classification for the five archipelagos in the Eastern Atlantic. Köppen-Geiger classification is provided in grey text within brackets (Agencia Estatal de Meteorología de España / Instituto de Meteorologia de Portugal, 2011; Cropper, 2013; García-Herrera et al., 2003; Peel et al., 2007; Tsalefac et al., 2015). The mean annual sea-surface temperature data between for 2009-2013 was obtained from http://data.unep-wcmc.org/datasets/36 and the mean annual precipitation for 1970-2000 from http://worldclim.org/version2.

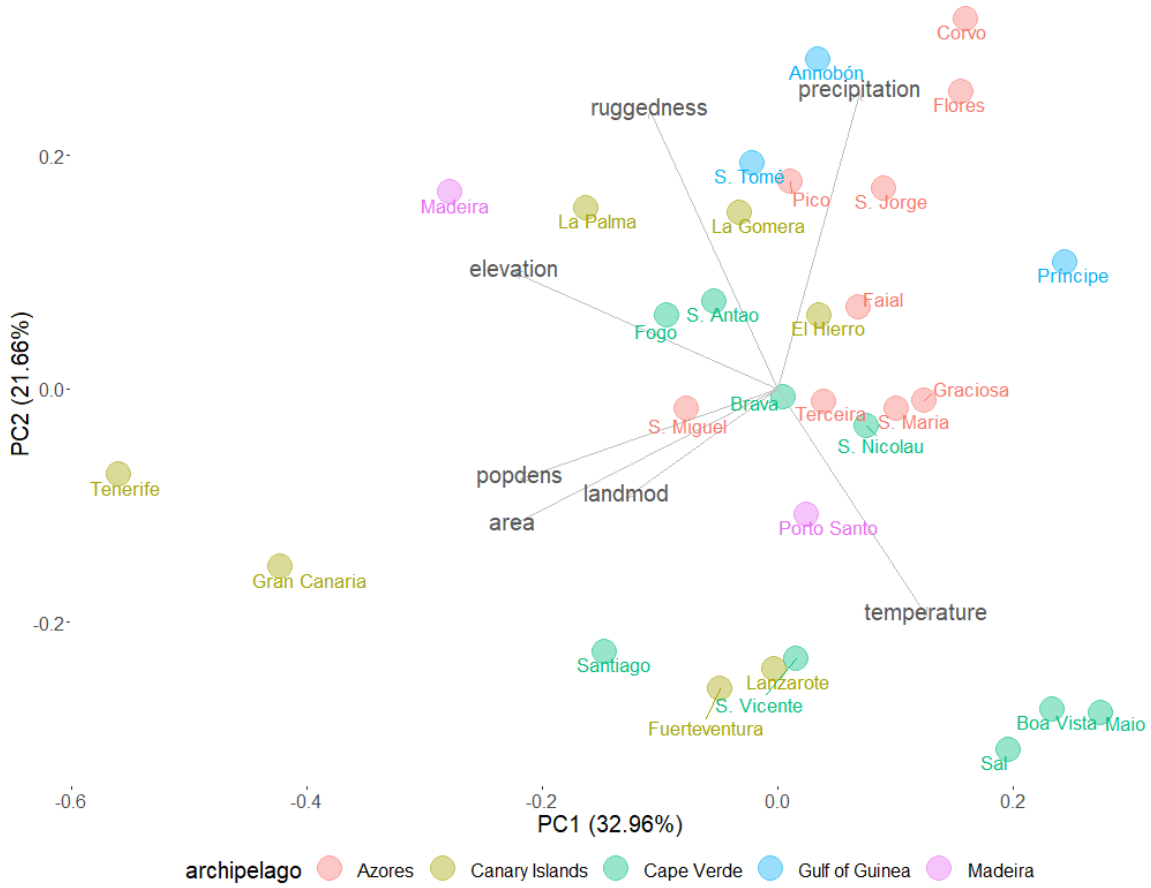

Figure A.2. Principal component analysis, first and second axis.

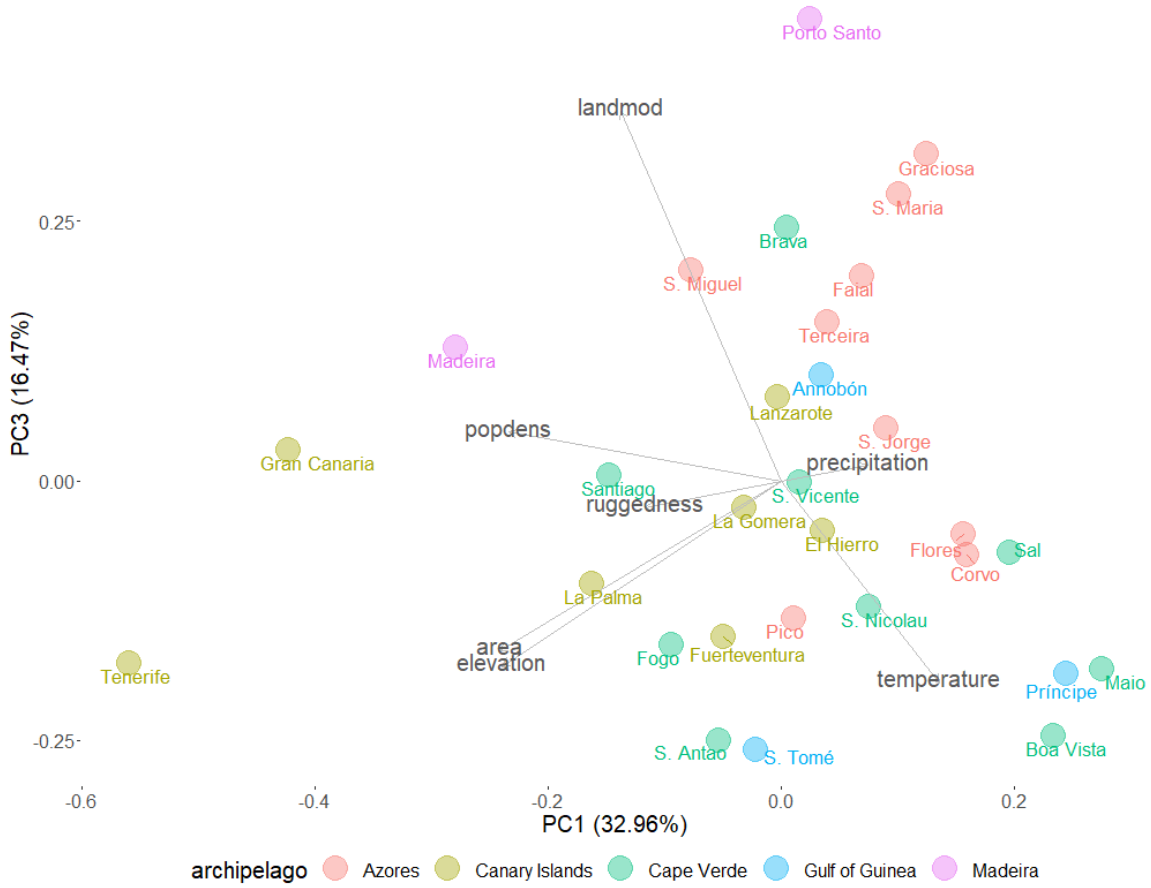

Figure. A.3. Principal component analysis, first and third axis.

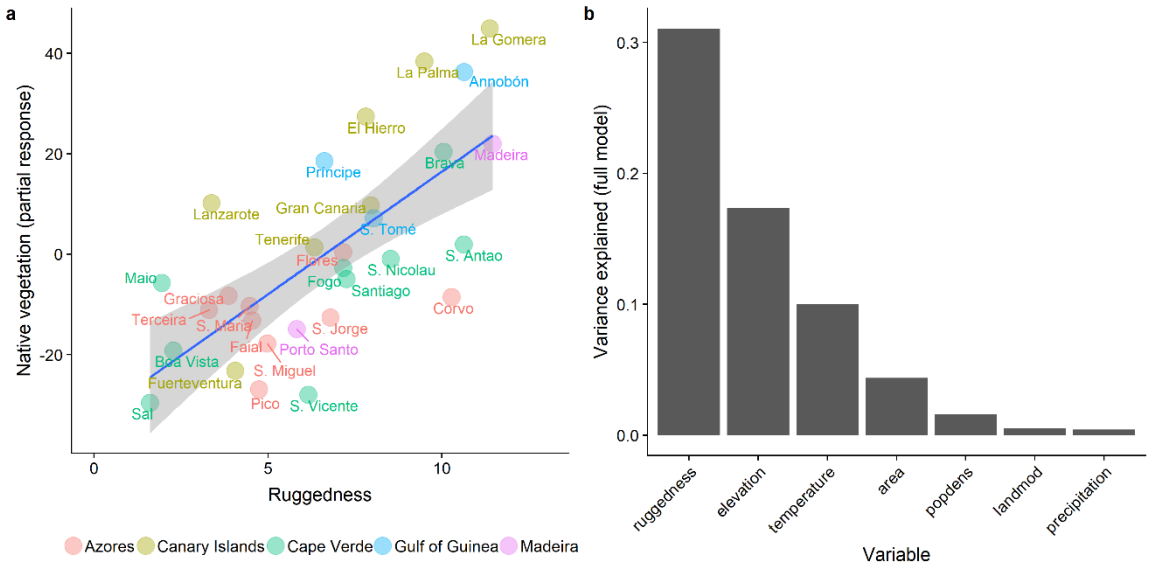

Figure. A.4. Complementary results of a multiple linear regression analysis showing the influence of environmental and societal variables on natural vegetation cover considering only remnant native forest patches in the Azores (Gaspar et al., 2011), ignoring all other native areas delineated in existing land use maps (Secretaria Regional do Ambiente e do Mar, 2007). a) Relationship between ruggedness and the partial response of native vegetation cover. b) Contribution of each predictor in the full model to the explanation of the variance in natural vegetation cover. The full model could explain 65.4% (R^2) of the variance, 31.1% of which is explained by ruggedness alone.

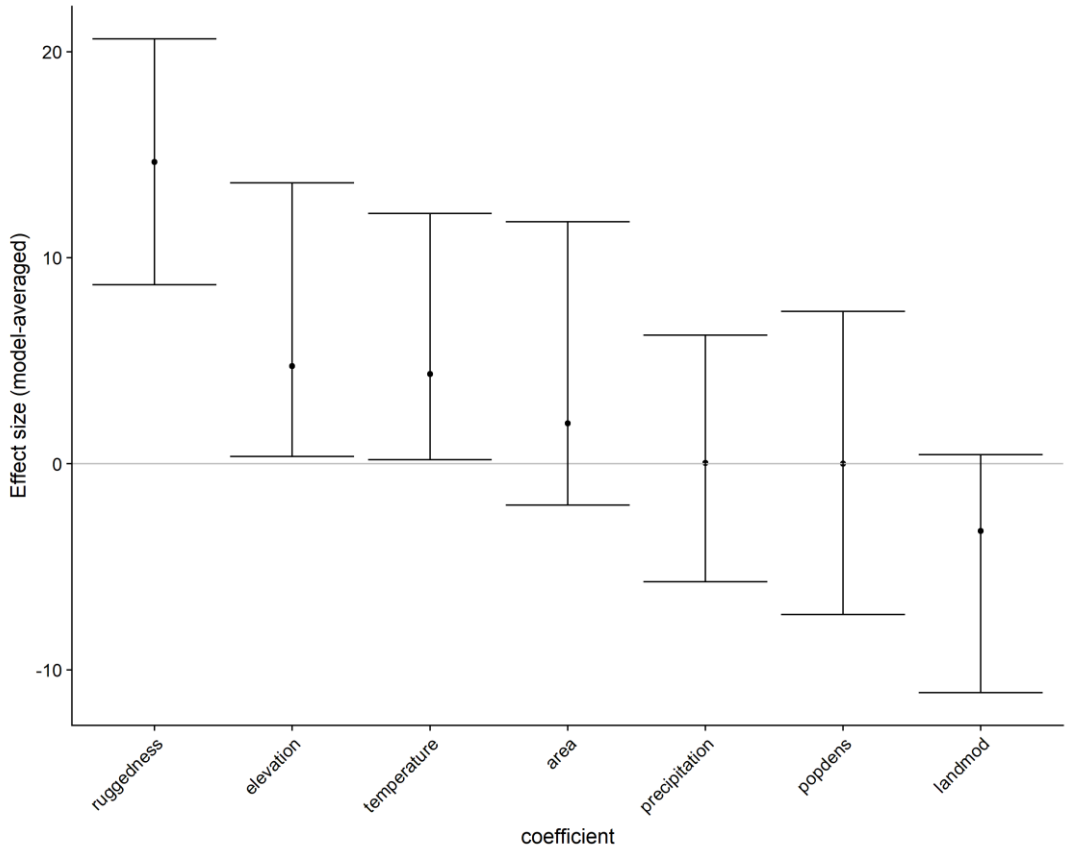

Figure. A.5. Effect sizes of model-averaged coefficients.

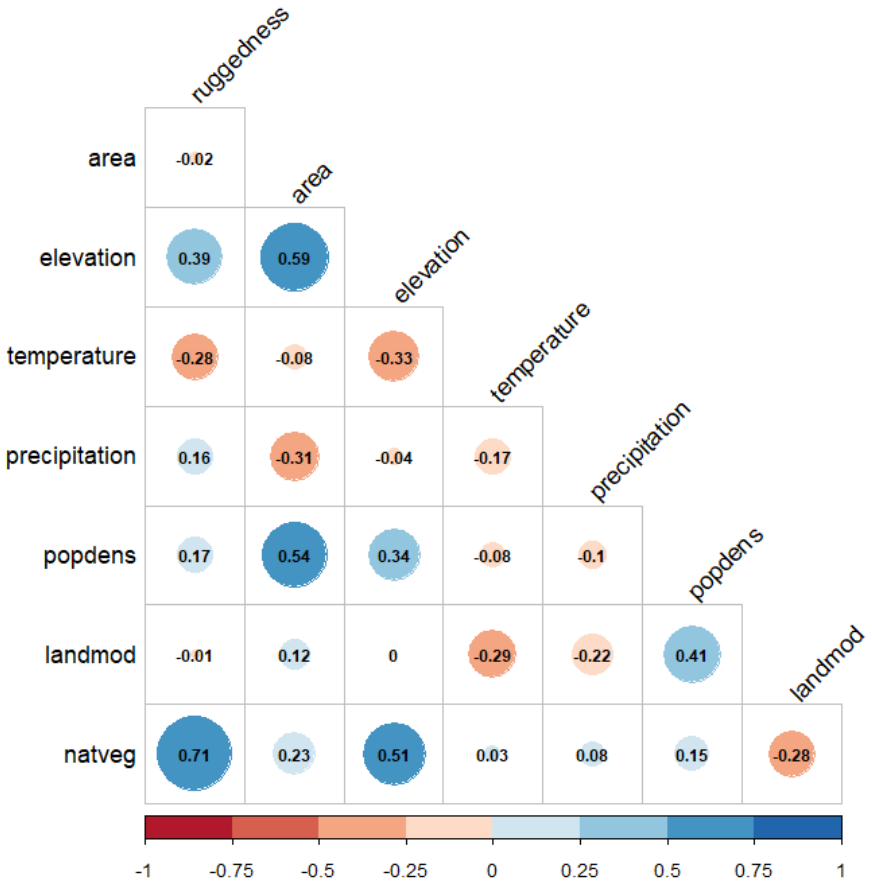

Figure. A.6. Correlations between variables related to topography (ruggedness, area, elevation), climate (temperature, precipitation), and society (population density, human landscape modification), together with native vegetation cover (natveg).

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